# THE REPRODUCTIVE CAPACITY OF PLANTS

*BY THE SAME AUTHOR*

THE LIVING GARDEN

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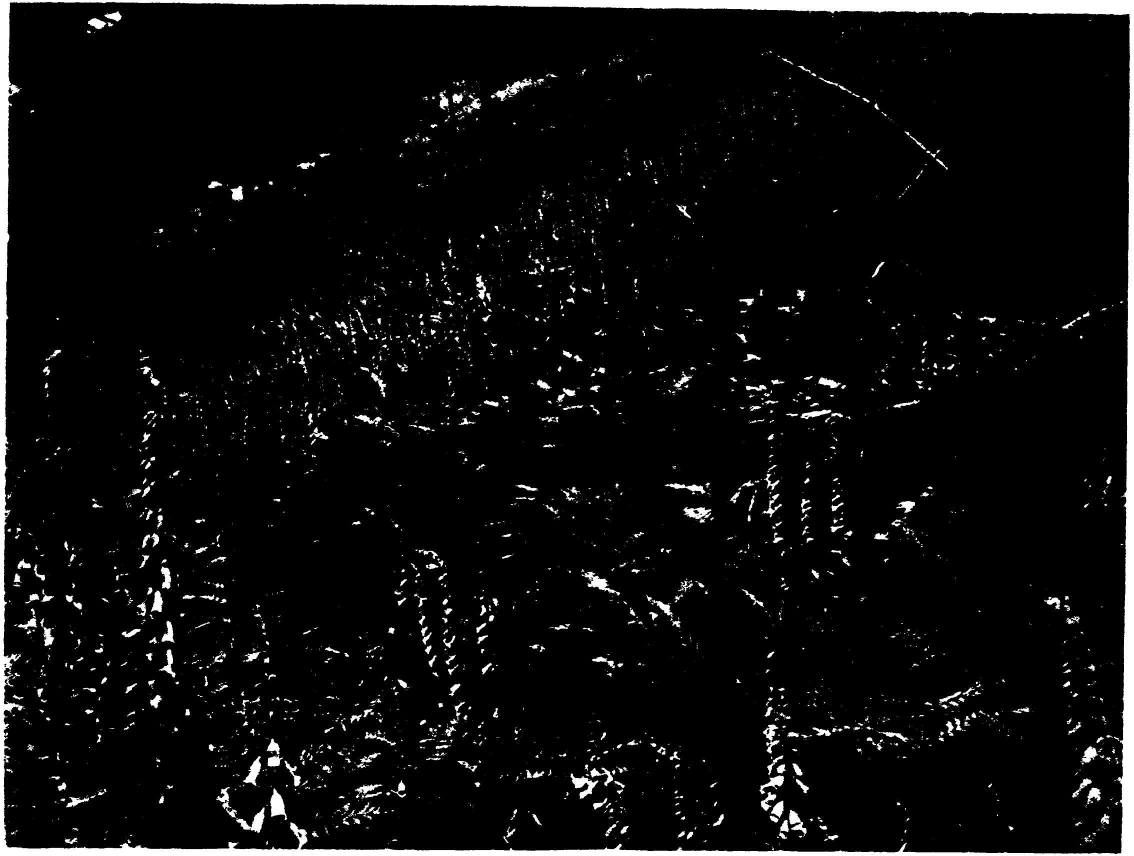

Foxgloves (*Digitalis purpurea*) in a felled woodland on a valley slope. Note their abundance in the foreground and distance and their absence beneath the uncut saplings in the middle distance (2 years after felling).

# THE REPRODUCTIVE CAPACITY OF PLANTS

*STUDIES IN QUANTITATIVE BIOLOGY*

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LONDON

G. BELL AND SONS, LTD

1942

*First published 1942*

Printed in Great Britain by William Clowes and Sons, Limited.
London and Beccles

# PREFACE

The reproductive capacity of a species is as much a characteristic as any other specific feature and one moreover of the greatest ecological importance. Nevertheless the subject is one that has been almost entirely neglected except by two or three investigators. This is mainly because reproductive capacity rarely has much value for purposes of identification and the collection of data is far more laborious than with respect to the other specific characteristics. With the growth of knowledge of the ecological relations of species, however, the need for filling this gap became increasingly apparent, and for a considerable period and especially during the past fifteen years I have collected such data whenever opportunity has offered. An interlude of relative leisure at the outbreak of the present war afforded me the opportunity to bring together these records of observations and experiments on the reproduction of British plants in their natural habitats.

I am indebted to my colleague, Professor R. A. Fisher, M.A., F.R.S., for suggesting that these results should be presented in the fuller and more accessible form possible in a book rather than in the journal of a learned society. I am also indebted to him for several helpful suggestions and for preparing the table on p. 20. I should also like to take the opportunity to record my appreciation of the readiness with which the Publishers undertook the production of this work and their helpful co-operation, and also that of the Printers, Messrs. Clowes and Sons, under the difficult circumstances of the present time.

As I venture to hope that the subject-matter will be of value not only to professional botanists but to others interested in our native plants and the biological problems they present, the English names as well as the Latin names have been given in the text. The inclusion of all but the most familiar of these popular names in the Index would have rendered this far too extensive, since data of one kind or another are furnished respecting nearly six hundred species, but the citation of the English names where these exist, in parenthesis, after the Latin binomials will, it is hoped, enable the Index to serve also as a glossary.

Some of the drawings in Fig. 4 have been based on illustrations of a paper by H. Becker, but all the other drawings as well as the photographs are original.

The publication of these data will, it is hoped, stimulate others to augment them and to fill the numerous gaps that still remain.

E. J. SALISBURY

The Athenaeum
March 1942

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# I

# INTRODUCTORY

There are perhaps few aspects of the study of plants that have received less attention than those pertaining to their vital statistics. Yet the importance of knowing the potentialities of different species with respect to their capacity for reproduction cannot easily be overemphasized. Darwin himself realized this importance, though his attention was drawn rather to the apparent superabundance of offspring with its consequential influence upon the struggle for existence than to the diversities between species in this respect. Indeed, the emphasis placed upon the fact that even the least prolific species would, if all its offspring survived, soon cover the entire land surface of the earth has tended to divert attention from the profound differences in the rates of reproduction of different species, and so the problem of the significance of these diversities has remained not only unanswered but almost ignored. The sparse data already available in botanical literature are nevertheless quite sufficient to show that species do vary greatly with respect to the number of viable seeds they produce, and one of the first questions which this fact raises is whether the respective abundance and frequency of different species is in any appreciable degree related to their respective potentialities for increase.

It has often been emphasized, *ad nauseam*, that every individual at death leaves, on the average, but one descendant, otherwise there would be a continual increase in the number of individuals. Actually, as we know, despite marked fluctuations in the numbers of individuals, species in undisturbed wild habitats do not exhibit any continuous augmentation. But here, as in many other similar generalizations, there is undue stress upon the average considered over a long period, and thus, by emphasizing the mean, we are led to neglect those fluctuations from the averaging of which our mean is derived and which biologically may be of far greater importance. We shall have to revert to this topic later, but for the moment we may note that if the approximate stability in the numbers of individuals, which is the essence of the above generalization, has anything of the significance that its frequent reiteration would suggest, either the diversity in numbers of potential offspring produced by different species has no biological significance whatever, and the most prolific species is merely the most wasteful and inefficient, or the potential progeny bears a definite relation to the natural mortality to which the species is normally subject.

If this latter view be correct, then of two species having seeds of equal viability the mortality, on the average, of the one producing, say, 100,000 seeds per annum must be approximately one hundred times as great as the mortality of a species which only produces an average of 1,000 seeds per annum. But, even if this be true over a long period of time, is the mortality higher in the former instance merely because there are more offspring eliminated in maintaining the observed stability of numbers, or is the larger number of potential

offspring a necessity imposed by an increased susceptibility to the natural causes of mortality? The latter view is that which may be considered the prevalent one, based mainly on the quasi-mathematical concept referred to above and on a few totally inadequate observations.

That a large seed output may be essential for the survival of a species is shown by *Fagus sylvatica.* Commonly seedlings of this tree only persist in Britain in " mast " years when the number of the progeny is so large that after the depredations of field mice and other enemies there still remains a residue that survive, whereas in the intervening seasons between the " mast years " the seedlings are entirely destroyed by their natural enemies. If the latter were to diminish in number a smaller output of seed would suffice for the survival of the Beech. It is tempting to assume that the process of natural selection has brought about a nicety of adjustment between the seed output and mortality, and this presumption is implicit in most of the writings on this topic. If true, it involves as a necessary corollary that the potential reproductive capacity of a species is a measure of its susceptibility to natural mortality. Such a relation, if it could be established, would at once place the numerical values representing the reproductive capacity of species in the front rank of biological data.

The object of the present inquiry, based upon the gradual accumulation of data during the past fifteen years, is to consider how far the current assumption is justified and to what extent reproductive capacity can be correlated with this and other factors, and, above all, to elucidate, if possible, its biological significance.

In various trees, besides the Beech, the survival of an unusual number of offspring is generally associated with the occurrence of " mast years," which suggests that the number of survivors bears some relation to the potential progeny. If this were generally true we might expect a rough relation to obtain between potential reproductive capacity and the abundance of a species. It is not, however, trees only that exhibit years of superabundant reproduction, since many herbaceous plants do, in certain seasons, produce an abnormal harvest of fruits or seeds, though usually the periodicity is less pronounced than for trees.

It is well known that with plant hosts, as with animals, an abnormal increase in the number of individuals is usually followed, though with a more or less pronounced lag, by an increase in the predators and parasites until a balance is again restored. It is, indeed, not improbable that *a pronounced fluctuation in numbers of offspring may have a definite survival value,* since an intermittent high reproductive capacity, owing to the lag in the increase of predators and parasites, might well increase the abundance of a species whereas a reproductive capacity maintained at the same high level would have little or no effect, since the plant enemies would likewise be maintained at a high level.

There is good evidence that external conditions, such as hot, dry summers, affect the fruiting of the Beech, but, though climatic factors may shorten or lengthen the interval between years of heavy production, it is evident that internal factors are involved in the tendency for the Beech to fruit heavily, on an average once every five to seven years, and for the Oak to exhibit a " mast

year" about once every five years. Even more striking is the periodic fruiting of certain Palms and Bamboos (W. Seifriz, 1920) associated with the monocarpic perennial habit. But the prolonged vegetative period, with all its dangers, culminating in a large production of seeds may be compensated by a relative immunity of the offspring from specialized enemies, of which a large population could alone survive if endowed with a precisely contemporaneous periodicity. The monocarpic perennials such as the Talipot Palm, *Corypha umbraculifera*, or the Bamboo, *Dendrocalamus*, are perhaps but extreme examples of a particular type of specialization brought about by natural selection, whereby a certain proportion of seedling mortality is evaded. It is relevant to note that " mast " years are often manifest in particular species over extensive geographical regions, and, as is well known, an exceptional year for a particular kind of fruit, such, for example, as 1940 for plums, is often characteristic of the entire country. On the other hand seasons of heavy yield may or may not be contemporaneous for different species. If, as we have suggested, the periodicity has a biological importance the facts just mentioned are entirely consistent with that view. Moreover such biological importance would be enhanced by the rather irregular character of the periodicity.

If the magnitude of the seed output is mainly the outcome of natural selection as determined by the average mortality, we should expect to find that species with a restricted type of habitat have a larger seed output than species whose requirements are less confined. For, except where there is a highly specialized method of seed dispersal which ensures transport of seeds to the precisely suitable locations, the more specialized the requirements of a species the larger will be the proportion of seeds that will reach unsuitable habitats and the greater will be the consequent wastage. This line of thought, coupled with the knowledge that the seed production of some specialized parasites was large, gave support to the view that seed production is mainly related to the chances of mortality. How far the view is correct that specialized parasites have larger reproductive capacities than the unspecialized, or either class of parasites than non-parasitic plants, will be considered later.

There is the further possibility that the seed output of a species is in the nature of a physiological accident quite independent of the immediate needs of the plant and governed chiefly by hereditary factors with little if any direct relation to survival value. The fact that different strains of cultivated crop-plants have been shown to differ in respect to yield, whilst it has demonstrated the heritable nature of this feature, is no evidence that it has little importance, since from the nature of these examples such strains are relatively immune from the operation of competition. In so far as any prevailing view can be said to be held on this topic, it is undoubtedly that reproductive capacity is correlated with the risks of mortality. The foregoing adumbration of the general problem shows, however, that it is less simple than has commonly been assumed, and, as the sequel will demonstrate, a number of features have to be taken into consideration before we can attempt to assess the biological significance of the reproductive capacity of a species.

# II

# THE SIGNIFICANCE OF SEED SIZE AND ITS RELATION TO HABITAT CONDITIONS

It is evident that for a plant of a given leaf area and therefore having a certain potentiality for photosynthesis the credit balance of food production may be expended on seed formation in one of two ways. Either the species may utilize the available food material for the production of a large number of relatively small seeds, each with but a very limited food supply to give the seedling its start in life, or there may be formed comparatively few seeds each with a copious food reserve, thus enabling the offspring to survive for a longer period before the necessity arises for them to be self-supporting. The former allocation has the advantage of tending towards wider dissemination and more probable occupation of all suitable habitats. Dispersal of small seeds is often more efficient than that of larger seeds and intraspecific competition is correspondingly reduced. Moreover, the large number of potential offspring is a greater insurance against the numerous adverse factors than when the potential number is few.

Large seeds though few in number have, however, the outstanding advantage of a sufficiency of food material to enable the germinating seedling to be independent, for a period that increases with the amount of food reserve, of its own photosynthetic activity, and so by being able to make more growth is better able to withstand the competition of other plants around it. It is evident that the large seed, with its copious provision of food, will be especially advantageous in closed communities where the colonizing individual must be capable of growing above the surrounding vegetation, or at least into a level of moderate illumination, before it can receive a sufficient intensity of light to manufacture its own food at a rate comparable to that of its neighbours.

An extreme example of the provision of a large food supply associated with a very limited reproductive capacity is afforded by the Double Coco-nut, *Lodoicea Sechellarum* Labill., which produces the largest fruits known. These weigh about 40 lb. each, but the low reproductive capacity which is the necessary concomitant of such lavish maternal provision is witnessed by the fact that this Palm only bears from four to eleven fruits at a time, they take ten years to develop, and the female trees do not begin to bear fruit until they are thirty years old (*cf.* Lindley and Moore, 1874, p. 692). These enormous fruits are carried by ocean currents, but, despite this, the difficulty of dispersal is confirmed by the restriction of the species to the two islands of Praslin and Curieuse. Nevertheless, although it breeds so slowly, the Palm persists in its restricted habitats, doubtless owing in large measure to the magnificent start in life which the offspring receive and their consequential high competitive capacity.

It is probably no mere accident that so many of the largest reproductive structures, whether fruit or seed, are associated with trees, for these are mostly

members of the late stages of plant successions, and thus their seedlings are more liable than those of most other categories of plants to have to make considerable growth before emerging into an illumination adequate for independent growth in the face of competition. At the other extreme of the scale we have plants such as the Orchids, which, as in the Acropera examined by Scott and referred to by Darwin, produce many millions of seeds in a single season.

It is evident that we have here two divergent methods by which provision is made for the continuation of the race, and in consequence there is necessarily a certain measure of negative correlation between seed number and seed size. But whilst this negative correlation must not be overlooked, and, indeed, is probably a significant factor in the comprehension of the problem before us, it is an aspect that may easily be overemphasized. It is probable that the more important aspect of the issues just raised is the relation to competitive efficiency.

To emphasize this, it may be well to consider more fully the extremely small seeds. These are especially characteristic of certain groups, of which the Orchidaceae, the Ericaceae, and the Pyrolaceae afford examples (*cf.* Fig. 1, 1–4). The seeds of these families mostly have weights that, expressed in grams, are in the sixth decimal place, so that the food provision for the germinating seedling is meagre in the extreme. Now all these groups are characteristically mycorrhizal, and I venture to think that the biological significance of the mycorrhizal habit has not received the attention it deserves though it is perhaps fundamental to the understanding of the phenomenon. The classical instance of the obligate relation in the Orchids has been shown to be a feature of the seedling phase, and the fungal partner may disappear from the adult. Moreover, it has been shown in this group that in appropriate organic media the presence of the fungus is not essential to good germination and subsequent growth. It would appear then that the fungus confers what may be described as a temporary saprophytism upon the chlorophyllous orchids, a condition that persists throughout life in the non-chlorophyllous types. It may be suggested that here, and in other mycorrhizal plants with small seeds, the feature is biologically important in that it confers this capacity to live saprophytically in the early stages of development and so enables a minute seed with practically no food reserves to develop nevertheless: it may be as an epiphyte, in the dim light of a tropical rain forest; as a terrestrial orchid, in the close turf of a chalk down; or as a pyrola in the dull illumination of a calluna heath or a pine wood. Yet each, despite the negligible food reserve, attains to sufficient size to become a photosynthetic plant. In other words the mycorrhizal habit in the seedling stage permits the production of minute seeds without the overwhelming handicap in competition which would otherwise accrue.

Two other classes of plants are also characterized by the possession of seeds of the same order of magnitude as these mycorrhizal types, namely the completely saprophytic plants and many parasites. This serves but to strengthen the view here advanced, since both are manifestly immune from the competition for light. It is true that whilst the seeds of a Broomrape (*Orobanche*) (Fig. 1, 5),

are of a weight similar to those of an Orchid, namely 0·0049 mg., the seeds of Cuscuta are appreciably larger and heavier, but these latter, on germination, have to live as independent plants, and may persist for seven days and form chlorophyll before a host plant is parasitized (*cf.* Pierce, 1894), whereas the the seeds of the Orobanche have been shown to germinate only in the immediate vicinity of the live roots of an appropriate host (*cf.* Tate, 1925). There are some seeds which are very light and which it is stated produce plants which are not mycorrhizal. Some of these are species of open habitats where competition for light is not appreciable. Such are the Sundews (*Droseras*), from which Frank stated mycorrhiza to be absent. The species of *Drosera* ger-

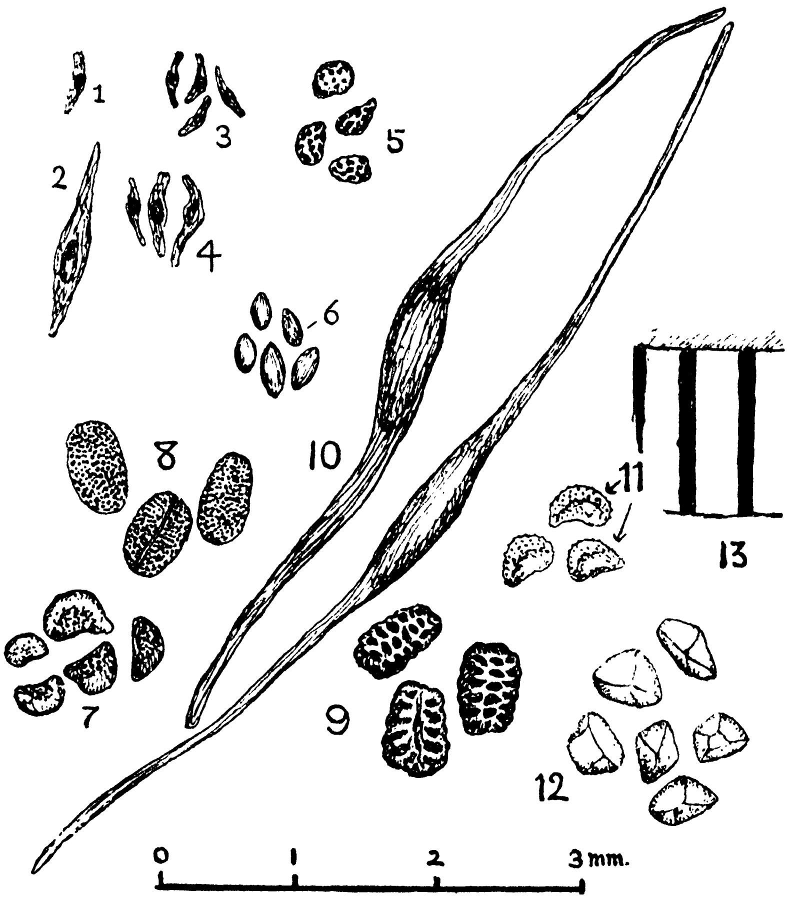



FIG. 1. SEEDS DISPERSED BY WIND (Figs. 1–5 and 7–10) and/or BY WATER (including rainwash) (Figs. 6, 11, and 12). 1. Sweet-Scented Orchis (*Gymnadenia conopsea*). 2. Sundew (*Drosera anglica*). 3. Lesser Wintergreen (*Pyrola secunda*). 4. *Pyrola media*. 5. Broomrape (*Orobanche elatior*). 6. *Tillaea muscosa*. 7. *Polycarpon tetraphyllum*. 8. Foxglove (*Digitalis purpurea*). 9. Figwort (*Scrophularia nodosa*). 10. Bog Asphodel (*Narthecium ossifragum*). 11. Red Spurrey (*Spergularia rubra*). 12. Brookweed (*Samolus valerandi*). All figures are drawn to the same scale, which is shown below, and in Fig. 13 the edge of a sixpence on the same magnification is shown for comparison.

minate in comparatively open communities, and occur, like most other rosette plants, where the illumination is appreciable. *Drosera rotundifolia* and *Drosera anglica* are indeed most abundant in the open conditions such as obtain after a moorland fire. It should, however, be mentioned that the writer when carrying out germination experiments with various species of *Drosera* found them to be remarkably tolerant, in the seedling stage, of a low light intensity. *Narthecium ossifragum* also has very light seeds (*cf.* Fig. 1, 10) and is also stated to be devoid of mycorrhiza and is to be found growing in dense plant communities. Concerning the physiology of both, more information is desirable, but it is pertinent to remark that though the adults of a species may be found in a closed and shaded community it does not therefore follow that the seedlings can become established under these conditions. Seedlings of Narthecium are usually to be found in comparatively open places, though, by vegetative spread from the adult, the species can extend in comparatively dense vegetation. This is perhaps true also for *Parnassia palustris*, which also has light seeds.

The light-seeded trees, such as the species of *Betula* and *Pinus*, are usually colonizers of more open situations, but both can and do colonize heathland, whilst the seedlings are usually found where the light can penetrate and is appreciable almost at ground level. The fact that the seedlings of both have been shown to grow better in the presence of the mycorrhizal fungus suggests that here too the small amount of food in the seed may have been rendered possible without detriment to the plant's chances of survival by reason of a facultative symbiotic relation.

It is evident that a large food supply may be advantageous for other reasons than to tide over a period of severe competition for light. Thus, in the shingle habitat the large seeds of *Lathyrus maritimus*, *Crambe maritima*, and *Honkenya peploides* enable the seedlings to send down an extensive root at an early stage of development, and this is true also of some sand-dune plants, such as *Cynoglossum officinale*, *Convolvulus soldanella*, and *Euphorbia paralias;* but it is, as the sequel will show, more frequent to find small seeds associated with open habitats.

In any attempt to assess the relationship that may obtain between seed size and habitat it is of course essential to consider the natural habitat of the species and not its artificial extensions. For instance, though *Galium aparine* is a species of the " marginal flora " of the woodland and of " scrub " it is almost equally common as a cornfield weed, where its possession of a large fruit is probably not essential for its maintenance.

Many small-seeded annuals which we most frequently associate with disturbed soil do also occur in natural habitats; such species, for example, as *Alchemilla arvensis*, *Trifolium minus*, *Arenaria leptoclados* are natural constituents of the flora of dunes, and are also to be found in dry pastures, where, owing to shallowness of the soil, its porosity or other adverse factors, the vegetation is sparse. It is also low in stature through the poor nutrition combined with the browsing of herbivorous animals. Thus, the herbage in which these annuals grow is a low open community with bare patches, where competition for light is negligible.

Consideration of the seed weights of a number of species, from communities of varying density and height, will serve to show in what measure these are correlated with habitat conditions. The significant community is clearly the most advanced type, *i.e.* the densest and tallest in which the species normally colonizes. For this reason I have mainly confined this survey to the British flora, since an intimate knowledge of the natural occurrence of the species concerned is essential. One important precaution in estimating the status of a species must, however, be stressed, namely the avoidance of the assumption that because adult plants of a species are present in a community of a particular density it is capable of colonizing under the same conditions. Species, especially those which have an efficient means of vegetative propagation, may persist and extend in dense communities, although reproduction from seed under the same conditions would not be possible and indeed only occurs where good conditions of illumination obtain. Examples are furnished by *Hypericum perforatum* and *Linaria vulgaris*, both of which, by virtue of their production of adventitious shoots from the lateral roots, spread effectively in comparatively dense herbage. The former is quite common in English Oak woods, but it is in the bare, well-illuminated areas, produced by coppicing, or naturally by the decay and fall of a tree, that the seedlings are to be met with. As very few ecologists have paid sufficient attention to seedlings of wild species to have acquired the capacity to identify them, the published records of their occurrence are practically non-existent, so that one is forced to rely almost entirely upon the limited data of one's personal experience. But it can probably be assumed that such errors of assessment as occur are mostly of the type already referred to, and that a species may have been assumed to colonize a denser community than it is actually capable of invading as a seedling. Such errors, if corrected, would tend to strengthen, rather than weaken, the evidence for the conclusions to which the data furnished lead us.

These data are in large part original observations based on seed samples obtained from the habitats cited. The comparatively meagre literature on seed weight has also been utilized both to supplement the number of species included and also where the seed weights obtained by the present writer differ from those recorded by other investigators. For most of these supplementary data I am indebted to the publications of A. A. Dallman (1933), M. A. E. Porsild (1920), Johannes Rafn (1915), and A. O. Stevens (1932).

In the accompanying tables the average weights of the seeds of various categories of plants are furnished, the sequence of these categories corresponding to an increasing competition for light to which colonizing seedlings are subjected, viz.: (1) Species of open habitats, where the degree of shading is at a minimum, and the seedlings, in their natural habitats, normally become self-supporting as soon as the first photosynthetic organs appear; (2) Species of the semi-closed or closed communities of short turf and pasture. Here, owing to the low height of the herbage, the seedling is normally only liable to any appreciable shading for a brief period of its early growth. In this section also are included meadow species, the position of which in the sequence is rather uncertain as the seeds of some meadow species only germinate where the community is more or less open, whilst other meadow species are more

shade-tolerant; (3) Species of scrub and woodland margin; (4) Shade species of the herbaceous flora of woodlands; (5) Woodland shrubs; (6) Woodland trees.

In each group there are appended the weights of the schizachenes of Labiateae and Umbelliferae, also the fruit weights of Compositae and Gramineae.

It is assumed that the seed weight is a rough approximation to the amount of the food supply available for the seedling, and thus affords some indication of the length of time the seedling can persist under conditions below the " compensation point."

Though not an exact measure, because of the varying thickness of the testas and the varying nature of the food reserves contained, with their different energy values, yet the approximation can be regarded as sufficiently accurate for the present purpose, particularly as it is the relative rather than the absolute values that are regarded as significant. The sources of error are naturally greater for the schizachenes and fruits, but it should be stressed that where these bear appendages (*e.g. Sanicula; Asperula*) they were removed, by abrasion before weighing, so as to render comparable the schizachenes and fruits in the various categories.

The plants of open habitats enumerated in Table I number ninety-eight. Of these the data for 59 species are additional to those already published. It will be noted that some of these species have extremely minute seeds, the average weight of those of *Sagina apetala* being only 0·0000075 gm., whilst those of *Tillaea muscosa*, *Juncus bufonius*, and *Polycarpon tetraphyllum* have an average weight of 12, 15, and 26 millionths of a gram respectively. The fruits of *Gnaphalium luteo-album* are also only 0·000015 gm. in weight. Apart from *Lathyrus Aphaca* the heaviest seeds are those of *Honkenya peploides*, *Cakile maritima*, and *Euphorbia paralias*, whilst the seeds of *Lathyrus maritimus* and *Convolvulus soldanella* (see Addendum), are also heavy ; but, as already indicated, there are special reasons why the possession of a large food reserve may be advantageous to such dune and shingle species, and it is noteworthy that this is more particularly a feature of the species capable of colonizing the younger phases of such habitats. Dune species with minute seeds, such as *Polycarpon tetraphyllum* (Fig. 1, 7) and *Phleum arenarium*, although found on bare dune soils usually occur on those which are more mature and capable of greater retention of water near the surface.

It will be evident from a perusal of the species listed that a wide range of well-illuminated habitats is represented and may be regarded as a fair sample of such situations. Of the seventy species of which seed weights are furnished the grand average is 0·00119 gm. The fruits of a further twenty-eight species average 0·001629 gm. and of all the propagules of the 98 species 0·001315 gm. It is manifest that if we had data of the actual seed weights instead of the fruit weights of the twenty-eight species their mean would probably be similar to that of the seeds.

Table II comprises the species of the semi-closed communities of short turf and pasture. There are also included in this table data respecting some species which not only occur in meadows but may perhaps be actually capable

| Species | Average seed weight in grams | | Habitat | Authority for weight |
|---|---|---|---|---|
| Anagallis arvensis L. | 0·000550<br>0·000522 | 0·000551 | Dunes and cultivated ground | Dallman<br>Salisbury |
| Anagallis foemina Mill. | 0·000581 | | Cornfields | ,, |
| Antirrhinum Orontium L. | 0·000180 | | Sandy fields | ,, |
| Arabis Turrita L. | 0·000617 | | Rocky places | ,, |
| Arenaria tenuifolia L. | 0·000042 | | Sandy fields | ,, |
| Atriplex patula L. (Seeds dimorphic) | 0·002150<br>0·000813 | 0·001481 | Cultivated ground | Stevens<br>Salisbury |
| Brassica arvensis (L.) Kuntze. | 0·0019<br>0·00202 | 0·00196 | ,, ,, | Stevens<br>Pammel |
| Brassica nigra (L.) Koch. | 0·0017 | | Cliffs and cultivated ground | Stevens |
| Cakile maritima Scop. | 0·01296<br>0·00892 | 0·01094 | Dunes | Guppy<br>Becker |
| Capsella Bursa-pastoris Medik. | 0·0001 | | Waste places | Dallman |
| Cardamine hirsuta L. | 0·000178 | | Dunes and cultivated ground | Salisbury |
| Chenopodium album L. | 0·0007<br>0·00059 | 0·00065 | Cultivated ground | Stevens<br>Salisbury |
| Chenopodium rubrum L. | 0·00006 | | Bare mud and cultivated ground | Stevens |
| Diplotaxis muralis DC. | 0·000279 | | Waste places | Salisbury |
| Erodium moschatum (L.) L'Herit. | 0·00222 | | Dunes | ,, |
| Erophila verna L. | 0·00359 | | Dunes and dry places | ,, |
| Erysimum cheiranthoides L. | 0·000125 | | Cultivated ground | Stevens |
| Euphorbia exigua L. | 0·00051 | | ,, ,, | Salisbury |
| Euphorbia Helioscopia L. | 0·00249 | | ,, ,, | ,, |
| Euphorbia paralias L. | 0·004727 | | Dunes | ,, |
| Euphorbia Peplus L. | 0·000497 | | Cultivated ground | ,, |
| Euphorbia portlandica L. | 0·0016 | | Dunes | ,, |
| Gentiana nivalis L. | 0·00003723<br>0·000015 | | Rocks | Porsild<br>Schroeter |
| Glaucium luteum Scop. | 0·00105 | | Shingle | Salisbury |
| Honkenya peploides Ehr. | 0·0161<br>0·01131 | 0·0137 | ,, | Guppy<br>Porsild |
| Hyoscyamus niger L. | 0·000792 | | Dunes | Salisbury |
| Juncus bufonius L. | 0·000015 | | Bare mud | Dallman |
| Juncus triglumis L. | 0·0000209 | | Alpine bogs | Porsild |
| Lathyrus Aphaca L. | 0·021 | | Cornfields | Salisbury |
| Limosella aquatica L. | 0·000009 | | Bare mud | ,, |
| Linaria Elatine Mill. | 0·0004 | | Cultivated ground | ,, |
| Linaria minor Desf. | 0·000065<br>0·000069 | 0·000067 | Waste places and cornfields | ,,<br>Dallman |
| Linaria spuria Mill. | 0·000394 | | Cultivated ground | Salisbury |
| Medicago minima L. | 0·000602 | | Sandy places | ,, |
| Montia lamprosperma Cham | 0·000277 | | Dry soils | Porsild |
| Nasturtium palustre DC. | 0·000096 | | Bare mud | Salisbury |
| Papaver Argemone L. | 0·000145 | | Sandy fields | ,, |
| Papaver dubium L. | 0.000128 | | Waste places | ,, |
| Papaver hybridum L. | 0·000158 | | Chalky fields | ,, |
| Papaver Rhoeas L. | 0·000138 | | Cornfields | ,, |
| Plantago Coronopus L. | 0·000155 | | Sandy ground | ,, |
| Plantago major L. | 0·0002 | | Waysides | ,, |
| Polycarpon tetraphyllum L. | 0·000026 | | Dunes | ,, |
| Reseda Luteola L. | 0·00021 | | Waste places | Dallman |

| Species | Average seed weight in grams | Habitat | Authority for weight |
|---|---|---|---|
| Roemeria hybrida L. | 0·000354 | Waste places | Salisbury |
| Sagina apetala Ard. | 0·0000075 | „ | Dallman |
| Sagina procumbens L. | 0·0000125 | „ | „ |
| Samolus valerandi L. | 0·000022 | Sandy places | Salisbury |
| Saxifraga oppositifolia L. | 0·00008916 | Rocks | Porsild |
| Sedum Rhodiola DC. | 0·0001543 | „ | „ |
| Sedum villosum L. | 0·0000185 | Wet places | „ |
| Silene acaulis L. | 0·0002483 | Rocks | „ |
| Silene noctiflora L. | 0·00085 } 0·00092 | Sandy fields | Stevens |
| | 0·001 | | Pammel |
| Silene nutans L. | 0·0004 | Rocks | Dallman |
| Silene quinquevulnera L. | 0·0005 | Sandy fields | Salisbury |
| Sisymbrium Thaliana Hook. | 0·0000309 | Dry fields | „ |
| Specularia hybrida DC. | 0·000335 | Chalky fields | „ |
| Spergula arvensis L. | 0·000322 | Cultivated ground | „ |
| Spergula sativa Boenn. | 0·00054 | „ „ | Dallman |
| Spergularia rubra (L.) Pers. | 0·000013 | Sandy places | Salisbury |
| Spergularia salina Presl. | 0·000075 | Salt marshes | Dallman |
| Stellaria media L. | 0·000505 | Cultivated ground | Salisbury |
| Thlaspi arvense L. | 0·000785 | | Stevens |
| | 0·00175 } 0·001245 | „ „ | Korsmo |
| | 0·0012 | | Salisbury |
| Tillaea muscosa L. | 0·000012 | Sandy places | „ |
| Trifolium arvense L. | 0·000393 | Sandy places. Dunes | „ |
| Trifolium suffocatum L. | 0·000237 | Dunes | „ |
| Veronica arvensis L. | 0·000122 | Dunes and waste places | „ |
| Veronica Buxbaumii Ten. | 0·000926 | Cultivated ground | „ |
| Viola tricolor L. | 0·0011036 | „ „ | „ |
| Viscaria alpina (L.) Fenzl. | 0·000051 | Rocks | Porsild |
| *Schizachenes* | | | |
| Aethusa cynapium L. | 0·00164 | Cultivated ground | Dallman |
| Bupleurum rotundifolium L. | 0·0023 | Chalky cornfields | Salisbury |
| Calamintha acinos Clairv. | 0·00044 | Dry places | „ |
| Mertensia maritima Don. | 0·001675 | Shingle | Porsild |
| Stachys annua L. | 0·001075 | Waste places | Salisbury |
| *Compositae* | | | |
| Gnaphalium luteo-album L. | 0·000015 | Sandy fields | Salisbury |
| Gnaphalium sylvaticum L. | 0·000026 | Clearings in woods | „ |
| Lactuca scariola L. | 0·00045 | Waste places | Stevens |
| Matricaria suaveolens Buchenau. | 0·00016 | Waysides | Dallman |
| Senecio Jacobaea L. | 0·00028 | Dunes and dry places | „ |
| Senecio viscosus L. | 0·00071 | Waste places | „ |
| Senecio vulgaris L. | 0·00016 | Dunes and waste places | „ |
| Sonchus asper Hill. | 0·0003 | Cultivated ground | |
| Sonchus oleraceus L. | 0·00042 | „ „ | „ |
| *Gramineae* | | | |
| Aira caryophyllea L. | 0·000174 | Dry places | Salisbury |
| Bromus sterilis L. | 0·0071 | Waste places | „ |
| Elymus arenarius L. | 0·0089 | Dunes | Porsild |
| Festuca ovina L. | 0·0006839 | Chalky soils | „ |
| Mibora minima Desv. | 0·0000685 | Damp sandy places | Salisbury |
| Phleum arenarium L. | 0·000117 | Dunes | „ |
| Poa annua L. | 0·0002 | Waste places | „ |

| Species | Average seed weight in grams | | Habitat | Authority for weight |
|---|---|---|---|---|
| *Other Fruits* | | | | |
| Alchemilla arvensis (L.) Scop. | 0·00019 | | Cultivated ground and dunes | Salisbury |
| Polygonum aviculare L. | 0·000675 | 0·001687 | Waste places | Stevens |
| | 0·0027 | | | Korsmo |
| Polygonum hydropiper L. | 0·00165 | 0·00207 | Bare mud | Stevens |
| | 0·0025 | | | Korsmo |
| Polygonum Persicaria L. | 0·0014 | 0·00205 | Cultivated ground | Pammel |
| | 0·0027 | | | Korsmo |
| Rumex acetosella L. | 0·000525 | 0·000412 | Waste places | Stevens |
| | 0·0003 | | | Korsmo |
| Rumex limosus Thuill. | 0·00043 | | Bare mud | Salisbury |
| Rumex maritimus L. | 0·000221 | | ,, | ,, |

| | | | | | |
|---|---|---|---|---|---|
| Mean weight for | 70 | species of | seeds of open habitats | 0·00119 | gm. |
| ,, ,, | 12 | ,, | schizachenes and other fruits | 0·001182 | ,, |
| ,, ,, | 9 | ,, | fruits of Compositae | 0·00158 | ,, |
| ,, ,, | 7 | ,, | fruits of Gramineae | 0·00246 | ,, |
| | | | Mean for fruits of 28 species | 0·001629 | ,, |
| | | | Mean weight of propagules of all 98 species | 0·001315 | ,, |

of colonizing in the taller and denser herbage that this implies. Whether, from the point of view of competition for light, the meadow should be regarded as a less favourable habitat than the woodland margin or scrub is problematical. The average seed weight for all the twenty-two species of short grass is 0·002214 gm. Of those which are features of meadows also the corresponding average is much higher, namely 0·0049 gm. Of the sixteen species of pastures for which fruit weights only are furnished, the mean weight is 0·00224 gm., a value not significantly different from that for the seeds. The Grasses alone show an average weight of 0·0008 gm., and if we compare the nine meadow species with the four that are definitely pasture species the average " seed " weight for the former is higher (0·00763 gm.) than that for the latter (0·000928 gm.). The lowest seed weights for the species in this category are those of *Erythraea umbellata* and *Gentiana lingulata v. praecox.* These, in common with other gentianaceous plants, are mycorrhizal species, and such, as already stated, are regarded as being in a different physiological category, so should perhaps have been excluded with *Chlora perfoliata,* which also has extremely light seeds (0·0000107 gm.), as well as *Gentiana nivalis,* from Table I. Apart from these, *Hypericum humifusum* has the lightest seeds of any of the short-turf species, and it is actually a moot point whether this should be placed here or in Table I, since the seedlings are perhaps only to be found in the bare areas.

Table III comprises the herbaceous species of the woodland margin and scrub, which characterize in fact the transitional phase from grassland to woodland. The shrubs themselves are not, however, included here, since their advent represents a later phase in this plant succession when the community is almost completely closed and the lower stratum of vegetation has

TABLE II. SEED WEIGHTS OF SPECIES OF THE SEMI-CLOSED OR CLOSED COMMUNITIES OF SHORT TURF AND PASTURE

| Species | Average seed weight in grams | Habitat | Authority for weight |
|---|---|---|---|
| Anthyllis vulneraria L. | 0·00229 | Chalk downs | T. J. Jenkin |
| Campanula rotundifolia L. | 0·00006 | Heaths | Porsild |
| Dianthus Armeria L. | 0·00258 | Dry banks | Salisbury |
| Dianthus deltoides L. | 0·00023 | Heaths | Dallman |
| Erythraea umbellata | 0·0000126 | Chalk downs | Salisbury |
| Gentiana lingulata C. A. Agardh. var. praecox (Townsend) Murb. (G. anglica Pugsley) | 0·000128 | Chalk downs | Salisbury |
| Geranium Columbinum L. | 0·0057 | ,, | ,, |
| Hippocrepis comosa L. | 0·00285 | ,, | ,, |
| Hypericum humifusum L. | 0·00002 | Heaths | Dallman |
| Juncus squarrosus L. | 0·0000275 | Damp heaths and moors | ,, |
| Lathyrus Nissolia L. | 0·00937 | Pastures | Salisbury |
| Linum anglicum Mill. (Linum alpinum v. anglicum) | 0·0024 | Chalk pastures | ,, |
| Medicago falcata L. | 0·00142 | Sandy heaths | ,, |
| Medicago lupulina | 0·0012 | Pastures | Stevens |
| | 0·00177 | ,, | T. J. Jenkin |
| Phyteuma tenerum Schulz. (P. orbiculare Auct. Angl.) | 0·000183 | Chalk pastures | Salisbury |
| Primula farinosa L. | 0·00009221 | Calcareous pastures | Porsild |
| Scilla verna Huds. | 0·00156 | Short turf by sea | Dallman |
| Silene Otites L. | 0·00018 | Sandy heaths | Salisbury |
| Trifolium repens L. | 0·000642 | Pastures | T. J. Jenkin |
| Veronica spicata L. | 0·000131 | Sandy heaths | Salisbury |
| Vicia angustifolia Roth. | 0·0182 | Dry pastures | Stevens |
| Viola lutea Huds. | 0·00145 | Upland pastures | Dallman |
| *Schizachenes and Achenes* | | | |
| Pimpinella saxifraga L. | 0·00169 | Pastures | Salisbury |
| Potentilla verna L. | 0·000166 | Limestone pastures | Dallman |
| Poterium sanguisorba L. | 0·00889 | Chalk pastures | T. J. Jenkin |
| Prunella vulgaris L. | 0·0006 | Pastures | Stevens |
| Salvia pratensis L. | 0·00102 | Chalk downs | Salisbury |
| Salvia horminoides Pourr. (S. verbenaca Auct. Angl.) | 0·00331 | Dry banks | ,, |
| Stachys germanica L. | 0·00087 | Roadsides | ,, |
| Stachys palustris L. | 0·000775 | Damp places | Stevens |
| *Compositae* | | | |
| Achillea millefolium L. | 0·0004 | Pastures | Stevens |
| Bellis perennis L. | 0·000154 | ,, | Salisbury |
| Carduus nutans L. | 0·00326 | ,, | ,, |
| Chrysanthemum Leucanthemum L. | 0·00022 | ,, | Stevens |
| Cirsium eriophorum (L.) Scop. subsp. anglicum Pitrak. | 0·0116 | ,, | Salisbury |
| Cirsium arvense (L.) Scop. | 0·001575 | ,, | Stevens |
| Senecio erucifolius L. | 0·0005 | ,, | Dallman |
| Taraxacum officinale L. | 0·000858 | ,, | Salisbury |

A. FRUITS OF PASTURE AND MEADOW GRASSES

| Species | Average seed weight in grams | Authority for weight |
|---|---|---|
| Agrostis alba L. | 0·00009 | Armstrong |
| Alopecurus geniculatus L. | 0·0002 | Stevens |
| Alopecurus pratensis L. | 0·00068 | T. J. Jenkin |
| Anthoxanthum odoratum L. | 0·000567 | Armstrong |
| Cynosurus cristatus L. | 0·000535 | T. J. Jenkin |
| Dactylis glomerata L. | 0·0009 | ,, |
| Festuca pratensis Huds. | 0·001712 | ,, |
| Festuca rubra L. | 0·0011 | ,, |
| Festuca elatior L. | 0·001706 | ,, |
| Lolium perenne L. | 0·00199 | ,, |
| Phleum pratense L. | 0·000371 | ,, |
| Poa pratensis L. | 0·00039 | ,, |
| Trisetum flavescens | 0·000346 | Armstrong |

Average weight of " seed " of pasture and meadow grasses 0·000814 gm.

B. SEEDS OF MEADOW PLANTS

| Species | Average seed weight in grams | Habitat | Authority for weight |
|---|---|---|---|
| Geranium pratense L. | 0·0099 | Damp meadows | Dallman |
| Lathyrus pratensis L. | 0·0136 | Meadows | Salisbury |
| Lotus corniculatus L. | 0·0012 | ,, | ,, |
| Lotus uliginosus Schk. | 0·000482 | Damp meadows | ,, |
| Onobrychis sativa Lank. | 0·010015 | Calcareous meadows and pastures | ,, |
| Plantago lanceolata L. | 0·00155 | Meadows and pastures | ,, |
| Trifolium pratense L. | 0·0019 | Meadows | T. J. Jenkin |
| Trollius europaeus L. | 0·00112 | Wet meadows | Dallman |

Average weight of seeds of eight meadow species 0·00497 gm.
,, ,, ,, twenty-two pasture species 0·002214 gm.

## TABLE III. HERBACEOUS SPECIES OF SCRUB AND WOODLAND MARGIN

| Species | Average seed weight in grams | Authority for weight |
|---|---|---|
| Aconitum anglicum Stapf. | 0·00362 | Dallman |
| Aquilegia vulgaris L. | 0·00195 | ,, |
| Arenaria trinerva L. | 0·000108 | Salisbury |
| Astragalus glycyphyllos L. | 0·00454 | ,, |
| Atropa Belladonna L. | 0·00141 | ,, |
| Bryonia dioica L. | 0·00943 | ,, |
| Campanula latifolia L. | 0·000261 | ,, |
| Campanula Trachelium L. | 0·00007 | Dallman |
| Digitalis purpurea L. | 0·00009 | ,, |
| Epilobium montanum L. | 0·00012 | Salisbury |
| Euphorbia esula L. | 0·0035 | Stevens |
| Geranium Phaeum L. | 0·0045 | Dallman |
| Geranium Sanguineum L. | 0·0123 | Salisbury |
| Hesperis matronalis L. | 0·002025 | Stevens |
| Hypericum Androsaemum L. | 0·0000625 | Salisbury |

| Species | Average seed weight in grams | Authority for weight |
|---|---|---|
| Hypericum hirsutum L. | 0·0000908 | Salisbury |
| Hypericum montanum L. | 0·000063 | ,, |
| Hypericum perforatum L. | 0·0001 | Dallman |
| | 0·000126 | Salisbury |
| Hypericum pulchrum L. | 0·00009 | Dallman |
| Luzula multiflora Lej. | 0·000418 (Clearings) | Salisbury |
| Melampyrum cristatum L. | 0·00975 | ,, |
| Melampyrum pratense L. v. hians Druce. | 0·00646 | ,, |
| Polemonium coeruleum L. | 0·00122 | ,, |
| Saponaria officinalis L. | 0·001375 | Stevens |
| Sisymbrium alliaria Scop. | 0·0034 | Dallman |
| Stellaria Holostea L. | 0·0037 | Salisbury |
| Tamus communis L. | 0·016 | Guppy |
| Veronica hybrida L. | 0·00018 | Dallman |
| Vicia hirsuta Koch. | 0·00417 | Salisbury |
| Vicia Orobus DC. | 0·025 | ,, |
| Vicia sepium L. | 0·01976 | ,, |
| Vicia tetrasperma Moench. | 0·0039 | ,, |

Average weight of seeds of thirty-two species of scrub and wood margin 0·004438 gm.

*Achenes and Schizachenes of Herbaceous Plants of Scrub and Woodland Margin*

| | | |
|---|---|---|
| Aegopodium Podagraria L. | 0·001993 | Salisbury |
| Anthriscus sylvestris Hoffm. | 0·00497 } 0·00468 | Dallman |
| | 0·00439 } | Salisbury |
| Ballota nigra L. | 0·00098 | ,, |
| Calamintha Sylvatica Bromf. | 0·000463 | ,, |
| Geum urbanum L. | 0·00205 | ,, |
| Heracleum Sphondylium L. | 0·01215 | Dallman |
| Nepeta Cataria L. | 0·000387 } 0·000443 | Salisbury |
| | 0·0005 } | Stevens |
| Stachys sylvatica L. | 0·0019 | Salisbury |
| Teucrium Scorodonia L. | 0·000409 | ,, |
| Torilis Anthriscus L. | 0·0019 (Abraided mericarps) | ,, |
| *Other Fruits* | | |
| Arctium minus Bernh. | 0·0075 | Stevens |
| Cirsium tuberosum All. | 0·00326 | Salisbury |
| Dipsacus pilosus L. | 0·0077 (Clearings) | ,, |
| Dipsacus sylvestris L. | 0·005 | ,, |
| Senecio sylvaticus L. | 0·0003 } 0·000345 | Dallman |
| | 0·00039 } (Clearings) | Salisbury |
| *Gramineae* | | |
| Bromus asper Murr. | 0·0071 | Salisbury |
| Milium effusum L. | 0·00138 | ,, |
| Poa nemoralis L. | 0·000197 | Armstrong |

Average weight of fruits of 15 species 0·003385 gm.
,, ,, ,, 3 species of Gramineae 0·002892 gm.

TABLE IV. SHADE SPECIES OF THE GROUND FLORA OF WOODLANDS

| Species | Average seed weight in grams | Authority for weight |
|---|---|---|
| Actaea spicata L. | 0·0067 | Salisbury |
| Adoxa moschatellina L. | 0·00071 | ,, |
| Allium ursinum L. | 0·00648 | Guppy |
| Arum maculatum L. | ·0·04536 | ,, |
| Colchicum autumnale L. | 0·0054 | Salisbury |
| Convallaria majalis L. | 0·0151 | ,, |
| Cyclamen europaeum Sm. | 0·0046 | ,, |
| Eranthis hyemalis Salisb. | 0·00235 | ,, |
| Euphorbia amygdaloides L. | 0·00405 | ,, |
| Hedera helix L. | 0·0259 | Guppy |
| Helleborus foetidus | 0·0088 | Salisbury |
| Helleborus niger L. | 0·0121 | ,, |
| Helleborus viridis L. | 0·011 | ,, |
| Iris foetidissima L. | 0·048 | Guppy |
| Leucojum aestivum L. | 0·05 | Salisbury |
| Luzula Forsteri D.C. | 0·00104 | ,, |
| Meconopsis cambrica Vig. | 0·00024 | Dallman |
| Mercurialis perennis L. | 0·0079 | Mukerji |
| Ornithogalum pyrenaicum L. | 0·0096 | Salisbury |
| Oxalis acetosella L. | 0·0024 | ,, |
| Paris quadrifolia L. | 0·00454 | ,, |
| Polygonatum multiflorum All. | 0·0282 | ,, |
| Polygonatum officinale All. | 0·0373 | ,, |
| Polygonatum verticillatum All. | 0·0296 | ,, |
| Primula acaulis Jacq. | 0·000681 | ,, |
| | 0·000778 | Guppy |
| Primula elatior Jacq. | 0·00085 | Salisbury |
| Scilla nutans Sm. | 0·006 | ,, |
| | 0·00532 | Dallman |
| | 0·00648 | Guppy |
| *Schizachenes* | | |
| Asperula odorata L. | 0·00495 (abraided) | Salisbury |
| Galeobdolon luteum Huds. | 0·0027 (does not fruit in shade) | ,, |
| Physospermum cornubiense D.C. | 0·0061 | ,, |
| Sanicula europaea L. | 0·0042 (without processes) | ,, |
| Pulmonaria longifolia (Bast) Kern. | 0·011 | ,, |
| *Fruits* | | |
| Ficaria verna Salisb. | 0·00135 | ,, |
| Melica nutans L. | 0·002564 | ,, |
| Festuca sylvatica Vill. | 0·001082 | ,, |
| Hordeum sylvaticum Huds. | 0·00416 | ,, |

Average of mean seed weights for 27 species 0·013686 gm.
Average of mean weights for schizachenes of 5 species 0·0058 gm.
,, ,, ,, fruits of 4 species 0·002289 gm.

an appreciably lower light intensity than when most of the herbaceous species first appear as seedlings. Of the thirty-two species for which the average weights are available the mean seed weight is 0·004438 gm., with a range from 0·0000625 for *Hypericum Androsaemum* to 0·025 for *Vicia Orobus*. The

achenes, schizachenes, and other dry fruits of fifteen species average 0·003385 gm., whilst the three grasses yield an average weight of 0·002892 gm.

Table IV gives the average seed weights of twenty-seven woodland species of the shade flora for which the collective mean is 0·013686 gm., with a range from 0·00024 for *Meconopsis cambrica* to 0·05 gm. for *Leucojum aestivum*. The schizachenes of five species average 0·00505 gm. and the " seeds " of three grasses 0·002602 gm.

TABLE V. WOODLAND SHRUBS

| Species | Average weight of seed or fruit in grams | Authority for weight |
|---|---|---|
| Berberis vulgaris L. | 0·0117 | Salisbury |
| Buxus sempervirens L. | 0·0131 | Johannes Rafn |
| Clematis vitalba L. | 0·00139 (fruits) | ,, |
| Cornus sanguinea L. | 0·0387 | Salisbury |
| Corylus avellana L. | 1·08 (fruits) | ,, |
| | 0·801 (kernels only) | ,, |
| Crataegus monogyna Jacq. | 0·08 | ,, |
| Crataegus oxycanthoides Thuill. | 0·0601 | ,, |
| Daphne mezereum L. | 0·069 | ,, |
| Euonymus europaeus L. | 0·0158 | ,, |
| Lonicera periclymenum L. | 0·004536 | Guppy |
| Prunus macrocarpa Wallroth | 0·193 (stones) | Salisbury |
| Prunus padus L. | 0·53 (stones) | ,, |
| Prunus spinosa L. | 0·0646 (stones) | ,, |
| | 0·05184 | Guppy |
| Rhamnus catharticus L. | 0·01292 | Salisbury |
| Rhamnus frangula L. | 0·0151 | ,, |
| Ribes grossularia L. | 0·005832 | Guppy |
| Rosa canina L. | 0·01605 (achenes) | Salisbury |
| | 0·019 | J. Rafn |
| Rosa rubiginosa L. | 0·0132 (achenes) | Salisbury |
| Sambucus nigra L. | 0·00257 | J. Rafn |
| | 0·00324 | Guppy |
| | 0·00476 | Salisbury |
| Sarothamnus scoparius (Koch) | 0·0076 | J. Rafn |
| Solanum dulcamara L. | 0·00135 | Salisbury |
| Ulex europaeua L. | 0·00675 | J. Rafn |
| | 0·006438 | Guppy |
| Viburnum Lantana L. | 0·0442 (stones) | Salisbury |
| Viburnum Opulus L. | 0·046 (stones) | ,, |

Total species 24. Range of average weight 0·00135–0·8 gm.
Grand average 0·085435 gm. (exclusive of *Corylus avellana* 0·050432 gm.).

Of the twenty-four species of woodland shrubs listed, the lowest average " seed " weight is that of *Solanum dulcamara* (0·00135 gm.) and the highest that of *Corylus avellana* (kernels only). The weight given for *Clematis vitalba* is that of the fruits without the styles, and it is quite likely, therefore, that the seed weight of this species would be below that of *S. dulcamara*. Of the species with succulent fruits the weights of the " stones " have been given. It is a moot point whether *Corylus avellana* should be included here, since, although an undoubted member of the scrub community, it can attain the

dimensions of a tree and is present in the climax phase. The grand average for all the twenty-four species is 0·085435 gm.

Table VI furnishes the average fruit or seed weights of twenty species of trees ranging from 0·00017 gm. for *Betula alba* to 4·05 for *Castanea vesca.* The grand average is 0·653 gm. It is clear that although this average would be appreciably reduced if seed weights, and not fruit weights, were available in all instances,yet the value would still remain very high.

TABLE VI. WOODLAND TREES

| Species | Average weight of " seed " in grams | Authority for weight |
|---|---|---|
| Acer campestre L. | 0·808 | Johannes Rafn |
| Alnus glutinosa Gaertn. | 0·00137 | ,, |
| Betula alba L. | 0·00017 | ,, |
| Carpinus Betulus L. | 0·0411 | ,, |
| Castanea sativa Miller | 4·05 | Maw |
| Corylus avellana L. | 1·08 (kernels only 0·801 gm.) | Salisbury |
| Fagus sylvatica L. | 0·225 | J. Rafn |
| Fraxinus excelsior L. | 0·07 | ,, |
| Pyrus communis L. | 0·0299 | ,, |
| Pyrus malus L. | 0·0329 | ,, |
| | 0·02582 | Guppy |
| Pinus sylvestris L. | 0·00559 | J. Rafn |
| Prunus avium L. | 0·175 | ,, |
| Quercus petraea (Matt) Liebl. (Q. Sessiliflora Salisb.) | 2·29 | Maw |
| Quercus robur L. | 3·853 | J. Rafn |
| Sorbus aria Sm. | 0·439 | ,, |
| Sorbus aucuparia Gaert. | 0·188 | ,, |
| Sorbus torminalis Ehrh. | 0·378 | ,, |
| Tilia parvifolia Ehrh. | 0·031 | ,, |
| Tilia platyphyllos Scop. | 0·087 | Maw |
| Ulmus montana Sm. | 0·0138 | J. Rafn |

Range of average weight of " seed " 0·00017–4·05 gm. Total 20 species.
Average of averages 0·653407 gm. (exclusive of *Corylus* 0·6309 gm.).
[*Aesculus hippocastrum* 11·5 gm.]

For convenience the grand averages for the various categories are summarized in the accompanying Table VIIa. From this it is evident that with increasing density of the plant community in respect to shade there is a marked tendency for the seed weight to be augmented. Furthermore, despite the much smaller numbers of species involved, it is worthy of note that the fruits show the same general trend, and it may therefore be inferred that this would apply to the contained seeds.

Assuming that the seed weight is a rough approximation to the supply of potential energy available for the seedling, we can state the above generalization in another form, namely that *in general the larger the supply of food material provided by the parent plant in the seed, or other propagule, the more advanced the phase of succession that the species can normally occupy.*

The averages are somewhat misleading, since they are markedly influenced

TABLE VIIa. SUMMARY OF AVERAGE SEED WEIGHT (IN GRAMS) OF SPECIES OF VARIOUS HABITAT CONDITIONS

| Open habitat species | Species of semi-closed or closed non-shady habitats | Meadow species | Herbs of scrub and wood margin | Shade species | Shrubs | Trees |
|---|---|---|---|---|---|---|
| *Seeds* | | | | | | |
| 70 species | 22 species | 8 species | 32 species | 27 species | 21 species | |
| 0·00119 | 0·002214 | 0·0049 | 0·004438 | 0·013686 | 0·0937 | — |
| *Fruits* | | | | | | |
| 30 species | 16 species | | 15 species | 6 species | 3 species | 20 species |
| 0·001629 | 0·00224 | — | 0·003385 | 0·00505 | 0·0107 | 0·6534 |
| *Gramineae* | | | | | | |
| 7 species | 13 species | | 3 species | 3 species | | |
| 0·00246 | 0·000814 | — | 0·002892 | 0·002602 | — | — |
| *All propagules* | | | | | | |
| 98 species | 51 species | | 50 species | 36 species | 24 species | 20 species |
| 0·001315 | 0·001862 | | 0·004029 | 0·011323 | 0·085435 | 0·6534 |

*Ratios of averages* (open habitat species as unity)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Seeds | 1: | 1·86 : | 4·1 : | 3·7 : | 11·5 : | 80 : | — |
| *All* propagules | 1: | 1·41 : | — : | 3·06 : | 8·6 : | 64·9 : | 496 |

by exceptionally heavy seeds and but little by exceptionally light ones. For this reason, and owing to the wide range of seed weights, the relation of these to habitat conditions is better realized if we group the seed weights in classes. The latter are so arranged that the upper limit of each is twice that of the preceding class. For this form of grouping I am indebted to my colleague, Professor R. A. Fisher, who kindly prepared Table VIIb (p. 20).

In interpreting this table it must be realized that the weight-class categories are of exponentially increasing magnitude. It is evident that the distribution with respect to each environment confirms the conclusions drawn from the means, since the proportions in the higher seed-weight classes increase as we pass from the left-hand to the right-hand column. We have pointed out that the meadow plants occupy a rather equivocal position in relation to the herbaceous plants of scrub, and moreover the numbers of species listed in this category are too few to provide more than an indication of the mean seed weight. With the sole exception of the meadow species, however, the mean scale values exhibit a continuous increase corresponding to the augmented shading which the seedlings are normally called upon to endure. Furthermore, in so far as a mode can be recognized, in the vertical columns corresponding to the different types of habitat, its position rises as we pass from the propagules of open habitat species to those of woodland trees.

Compared with the seed-weights of open habitat species, those of the progressively more advanced habitats are seen to augment, at first steadily then rapidly.

Whether the heavier propagules in the more closed and taller vegetation types represent a direct adaptation to these environments or whether it is only

TABLE VIIb. Summary of data of weights of all types of propagules. The class intervals are arranged in ascending order from 1 to 24: The upper limit of each class is twice that of the upper limit of the preceding class (Class 3=0·00000381 gm. to 0·00000763 gm. Class 24=eight to 16 gm.).

| Class | Open habitat | Short Turf | Meadow | Scrub | Woodland he bs | Shrubs | Trees |
|---|---|---|---|---|---|---|---|
| 24 | | | | | | | 1 |
| 23 | | | | | | | 1 |
| 22 | | | | | | | 2 |
| 21 | | | | | | 1 | |
| 20 | | | | | | 1 | |
| 19 | | | | | | | 2 |
| 18 | | | | | | 1 | 3 |
| 17 | | | | | | 2 | 3 |
| 16 | | | | | 4 | **5** | 1 |
| 15 | 1 | 1 | | 3 | 3 | 2 | 3 |
| 14 | 3 | 3 | 3 | 4 | 7 | **5** | 1 |
| 13 | 2 | 1 | | **9** | **10** | 4 | 1 |
| 12 | 7 | 7 | | **9** | 4 | 1 | — |
| 11 | 10 | **10** | 4 | 8 | 3 | 2 | 1 |
| 10 | 15 | **10** | | | 4 | — | — |
| 9 | **17** | 4 | 1 | 6 | — | — | — |
| 8 | **18** | 9 | — | 2 | 1 | — | 1 |
| 7 | 8 | 1 | — | 9 | — | — | — |
| 6 | 4 | 1 | | | | | |
| 5 | 6 | 2 | | | | | |
| 4 | 6 | 1 | | | | | |
| 3 | 1 | 1 | | | | | |
| Species | 98 | 51 | 8 | 50 | 36 | 24 | 20 |

| | Mean scale value | Standard error | Variance |
|---|---|---|---|
| Open habitats | 8·786 | ±0·276 | 7·486 |
| Short turf and pasture | 9·921 | ±0·332 | 5·594 |
| Meadow species | 11·875 | ±0·665 | 3·554 |
| Scrub and wood margin | 10·940 | ±0·358 | 6·425 |
| Woodland herbs (shade fl.) | 12·944 | ±0·328 | 3·825 |
| Shrubs | 15·000 | ±0·511 | 6·041 |
| Trees | 17·050 | ±0·881 | 15·839 |

those species which possess heavier types of seed that can survive therein, the data leave no room for doubt that there is an association of seed weight with habitat conditions. The progressively steeper character of the rising curve of seed weight is in harmony with the suggested relation to conditions of illumination. The degree of shading at ground level shows a similar augmentation when we compare open habitats, grasslands, scrub, and woodland.

It need scarcely be emphasized that there are some striking exceptions to these generalizations, but at least some of these are more apparent than real. Attention has already been drawn to the special advantages that may accrue to certain sand dune plants and species of shingle beaches as an outcome of the possession of relatively large seeds, by enabling them to develop an extensive root system at an early stage. Furthermore, a large seed or fruit may be

advantageous to a pioneer species of shingle, or even dune, as being less readily carried down by rain too far below the surface. As such seeds are usually dispersed by the tide or blown along the sand surface by the wind the larger size does not involve a handicap to adequate dissemination.

The possession of a large food reserve must, in itself, always be advantageous, although it may involve indirect drawbacks. Since, however, the species of more open habitats do not in fact produce heavy seeds as a general rule, but, proportionally to their size, a large number of small ones, we are led to believe that an augmented seed output must have a survival value despite the small proportion of the offspring that are destined to persist to maturity.

A number of the species found in coppiced areas of woodlands, although associated with a late phase of succession, possess very small seeds, which, however, germinate only under favourable conditions of illumination such as coppiced areas afford. *Verbascum Thapsus* and *Digitalis purpurea* are both species of the woodland margin often seen growing amidst tall herbage; but the conditions when they actually germinated were probably very different, for, as Kinzel showed, the seeds of both these species require adequate illumination to bring about germination. Both these species have very small seeds, and, in relation to their habitat, may be described as opportunists, their very large seed output enabling them to achieve success in this role. In common with other species of the wood margin they are, in fact, colonizers of intermittently open habitats. Clearly such species are in quite a different category to *Actaea spicata* or *Leucojum vernum*, which have large seeds, and which, according to Kinzel (1909), germinate better in the dark than in the light; or species such as *Chrysosplenium oppositifolium* or *Trientalis europea*, respectively characteristic of alder woods and pine woods, which, though they have seeds that germinate better in the light, nevertheless exhibit an appreciable germination in darkness.

Attention may be drawn to the role of three of the tree species in the list, as pioneers. *Betula alba*, *Pinus sylvestris*, and *Fraxinus excelsior* are all especially frequent as saplings in clearings of woodlands and their seedlings are usually met with in the better-lighted areas. This is especially true of the first two, both of which have very small seeds for trees and exhibit mycorrhiza in the seedling stage.

It is relevant to note that Hesselman in a recent paper (1939) has furnished evidence that the Spruce, which, like the Birch, has very light seeds, containing, for an aboreal species, a very small food supply, exhibits a positive correlation between the vigour of the saplings and the illumination of the stand, the chief difficulties in establishment of this species being attributed to the herbaceous ground flora rather than to soil conditions.

Another very light-seeded forest tree is *Populus tremula;* but this, so far as Britain is concerned, apparently never produces fertile seeds and owes its frequency and success to vegetative propagation by root shoots, which, having the resources of the parent plant to draw upon, can grow up successfully even amongst tall and dense vegetation. Vegetative propagation has this important advantage for species of shady habitats, that a larger supply of food material is usually available for the new individual, a feature well seen

in *Mercurialis perennis,* of which the seed production is extremely sparse but the vegetative propagation lavish. Perhaps even more striking is the abundance of the tetraploid strain of *Ficaria verna,* which reproduces mainly by bulbils, and the comparative scarcity of the diploid which produces seeds (Marsden-Jones, 1935). In *Dentaria bulbifera,* although flowers are produced seeds do not develop, reproduction being entirely by means of the axillary bulbils, which are of considerable size and provide ample reserves for the development of the young plant in the better-lighted areas of the beech woods which this species frequents.

A particularly striking example is afforded by *Epilobium angustifolium.* This species is often found in abundance in beech woods, though only in the better-illuminated areas, and yet, like its congeners, produces seeds which though numerous are very light. Actually the seedlings only become established in the better-illuminated areas, largely owing to the necessity for the light itself, but further because, as a nitratophilous species, growth is depressed in the shadier situations where nitrates are usually sparse. Coppiced or burnt areas are the most likely situations to find seedlings, but the spread into more shady situations and extension after a coppiced area has grown up is due to the vegetative spread by means of shoots from the underground organs. It is thus not the exception to the relation between seed weight and habitat that superficially it would appear to be.

In general it is true that the species of open habitats are commonly annuals whilst the later phases of the plant succession are predominantly populated by perennials which tend to attain their largest dimensions in the climax phase. Thus it might appear that the increase in seed weight is a concomitant of duration and habit rather than a direct correlation with habitat conditions. It is, of course, manifestly true that the larger the plant the more likely it is to be capable of producing seeds with large food reserves without detriment to the number requisite for the maintenance of the species. Hence the large woody perennials are not only by their size suited to the climax phase but are better equipped for producing the larger seeds which, it is suggested, the closed community necessitates, unless the possession of mycorrhiza or some other physiological specialization renders a large food reserve for the seedling superfluous. But, if we compare species within the same genus, it is at once obvious that though the annual species commonly have the lighter seeds and are associated with open habitats they do sometimes produce heavy seeds. This is well seen in the genus *Euphorbia* (*cf.* Fig. 2) where, of the species which occur in Britain, the heaviest seeds are produced by *Euphorbia Lathyris,* an annual or biennial species, which although mostly found in open habitats, such as cultivated ground, can, as Hooker mentions, be found in copses. Both the woodland species *Euphorbia amygdaloides* (0·00405 gm.) and *Euphorbia hiberna* are perennial and have large seeds, but *Euphorbia portlandica,* which is also perennial but a plant of open habitats, has small seeds that weigh only 0·0016 gm., that is, less than half the weight of the woodland species. On the other hand, though most of the annual species of open habitats have very small seeds (*e.g. E. peplus, E. exigua* (0·00051 gm.), as well as the continental *E. peploides, E. Preslii, E. Chamasyce,* and *E. Pterococca*), yet *Euphorbia*

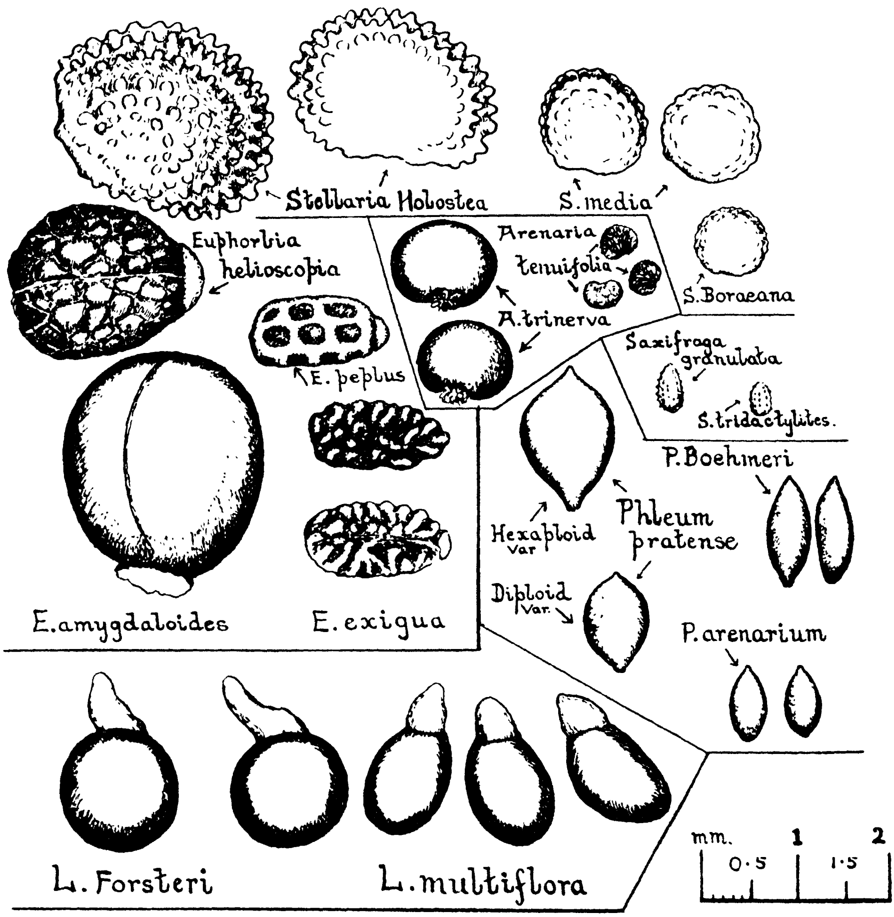



FIG. 2. SEEDS OF SPECIES OF OPEN AND MORE OR LESS CLOSED COMMUNITIES BELONGING TO THE SAME GENUS

Chickweeds, *Stellaria Boraeana*, a species of sand dunes, *S. media*, of cultivated ground and semi-open habitats, *S. Holostea*, a woodland plant. Sandworts, *Arenaria tenuifolia*, a species of open habitats, and *A. trinerva*, a woodland species. *Saxifraga tridactylites*, a dune species, and *S. granulata*, a species of meadows. Spurges, *Euphorbia exigua*, *E. peplus*, and *E. helioscopia*, species of cultivated ground, and *Euphorbia amygdaloides*, a woodland species. Cat's-tail Grasses, *Phleum arenarium*, a sand dune species, *P. Boehmeri*, a species of short turf, and *P. pratense*, a meadow species. Woodrushes, *Luzula multiflora*, a species of light patches and coppiced woodlands, and *L. Forsteri*, a species of partial shade. Note the smaller-sized seeds of the open habitat species.

*helioscopia*, which is also an annual, produces large seeds of an order of size approaching that of the woodland perennials (0·00249 gm.). One genus of which seed weights are available for a number of species and which also furnishes an adequate range of seed weight for our purpose, as well as a considerable range of habitat, is the genus *Trifolium*. The seed weights of some thirty members of this genus were published by Harshberger (1922), who gave the weights of ten seeds in milligrams, quoted below. These data are here grouped into those of open habitats and those of more or less closed habitats.

TABLE VIII. WEIGHTS OF SEEDS OF *TRIFOLIUM* SPECIES (after Harshberger)

A. SPECIES OF MORE OR LESS CLOSED COMMUNITIES

| Species | Habitat | Weight in milligrams of 10 seeds |
|---|---|---|
| T. subterraneum | Gravel pastures (annual) | 26–119·6 |
| T. incarnatum | Pastures (annual) | 30–42·5 |
| T. pannonicum | Meadows | 28–41 |
| T. maritimum | Maritime pastures (annual) | 15–25 |
| T. pratense | Meadows (perennial) | 13–25 |
| T. striatum | Dry pastures (annual) | 20–20·6 |
| T. rubens | Open woods | 18–23·5 |
| T. squarrosum | Meadows (annual) | 15 |
| T. tridentatum | Meadows | 13·5 |
| T. medium | Wood margin (perennial) | 12·5–13 |
| T. alpestre | Pastures and mt. woods (perennial) | 10–15·5 |
| T. montanum | Meadows (perennial) | 5–11 |
| T. hybridum | ,, ,, | 5·5–8·8 |
| T. elegans | ,, ,, | 4·5–7·5 |
| T. reflexum | Meadows (annual) | 6–6·5 |
| T. patens | Damp meadows (annual) | 6·5 |
| T. repens | Meadows (perennial) | 2–8 |
| T. spadiceum | Alpine pastures (annual) | 5 |
| T. aureum | Clearings in woods (annual) | 3 |

Mean for 19 species 1·7 mg. per seed. $\sigma$=2·0; S.E.M.=0·35

B. SPECIES OF OPEN COMMUNITIES

| | | |
|---|---|---|
| T. alexandrinum | Sandy beaches | 30–34 |
| T. angustifolium | Stony places (annual) | 12–14 |
| T. filiforme | Dry, open pastures (annual) | 4·5–5·6 |
| T. Bocconii | Dry, open places (annual) | 3–5·5 |
| T. minus | Dry, open pastures (annual) | 3–3·5 |
| T. procumbens | ,, ,, ,, ,, | 2·5–5 |
| T. agrarium | Dry fields (annual) | 2–5 |
| T. arvense | Dry sandy places (annual) | 2–4 |
| T. scabrum | Sandy places (annual) | 1–4·5 |
| T. dubium | Waste places (annual) | 3·3 |
| T. glomeratum | Sandy places (annual) | 2·5–3 |
| T. spumosum | Dry places (annual) | 2·5 |
| T. cernuum | Waste places (annual) | 2 |
| T. suffocatum | Dunes | 2·3 (E. J. S.) |

Mean for 14 species 0·59 mg. per seed. $\sigma$=0·8; S.E.M.=0·16
Difference of means=1·11; S.E.D.=0·38

Whilst the relation between seed weight and habitat in *Trifolium* is very striking and is quite in conformity with the views already put forward, yet it will be noted that the two species with the heaviest seeds are annuals. In fact, the species listed show little correlation between seed weight and duration, although most of the open habitat species have light seeds and are annuals.

The conclusion seems obvious that in so far as the small seed and the annual habit go together they are both features which probably alike have survival value in habitats that are subject to annually recurrent adverse conditions. Thus, the effect of artificial disturbance by cultivation in arable land or a garden is evaded by the seed stage equally with the recurrent summer drought of sandy or other dry soils; whilst the open character of these habitats, by not imposing the necessity of large food reserves in the seeds, renders their small size innocuous and a proportionately larger output possible.

Finally, in view of the very considerable diversity of species represented in the habitat lists previously dealt with, it may be well to draw attention to the general feature that if we compare the weights of the seeds or fruits of species of the same genus it will be found that the heavier are usually those of the species associated with the more closed and/or shaded type of plant community. The following table of congeners illustrates this feature and includes some species additional to those in the foregoing lists (*cf.* Table IX and Figs. 2 and 3).

The ratio of the averages for the two groups of species is 2·23; moreover, it will be seen that of the thirty-two genera represented only four present a higher weight for the more advanced type of habitat. Such exceptions are due to the fact that a large food supply in the seed is in itself advantageous in all types of habitat and particularly so in some.

Since the smaller the size of the seed the larger the number that can be produced with the same food supply it follows that small seed size can confer what may be described as *advantages of position.* All very small seeds are effectively dispersed, and hence the larger their number the more will be likely to attain situations where competition is too slight to inhibit establishment of the seedlings. On the other hand, the large seed, with its usually less wide dispersal, is not a reproductive mechanism that normally evades competition, but which, according to the measure of its contained food, enables the seedling [illegible]t it. Considered individually, without regard for their numbers, the [illegible] of survival must increase with the increase of reserve food-material in the seed. Conversely, the smaller the reserve the more likely the seedling is to be suppressed, so that, since decrease in size of seeds is usually accompanied by an increase of the average seed output, it can be said that to this extent support is furnished for the view that seed production is augmented with the risk of non-survival. But we have also seen that increase of seed weight is generally associated with normal habitat conditions where the plant community is denser and/or taller, that is, increasing seed weight is usually associated with increasing severity of competition, so that from this aspect decrease of seed output is associated with increase of risk of mortality. Clearly, then, if seed production be at all closely related to the risk of mortality, seed weight is also involved, and the measure of such risk will be proportional to

| Species of open or less shaded habitats | Weight in grams | Congeners of more closed and/or shaded habitats | Weight in grams | Difference |
|---|---|---|---|---|
| Alopecurus agrestis (arable) | 0·00105 | Alopecurus pratensis (meadows) | 0·00068 | −0·000370 |
| Arenaria tenuifolia (open) | 0·000042 | Arenaria trinerva (woods) | 0·000108 | 0·000066 |
| Astragalus danicus (dunes and turf) | 0·0011 | Astragalus glycyphyllos (woods) | 0·00454 | 0·00344 |
| Asperula cynanchica (downs) | 0·0016 | Asperula odorata (woods) | 0·00495 | 0·00335 |
| Bromus sterilis (open) | 0·0071 | Bromus asper (scrub) | 0·0071 | 0·000 |
| Calamintha acinos (open) | 0·00044 | Calamintha sylvatica (scrub) | 0·000463 | 0·000023 |
| Campanula rotundifolia (open) | 0·000060 | Campanula latifolia (scrub) | 0·000261 | 0·000201 |
| Euphorbia exigua (arable) | 0·00051 | Euphorbia esula (scrub) | 0·0035 | |
| Euphorbia helioscopia (arable) | 0·00249 | Euphorbia amygdaloides (woods) | 0·00405 | |
| Euphorbia paralias (dunes) | 0·004727 | Euphorbia Lathyris (woods) | 0·026 | |
| Euphorbia peplus | 0·000497 | | Av. Diff. | 0·009215 |
| Euphorbia portlandica (dunes) | 0·0016 | | | |
| Festuca ovina (open) | 0·0006839 | Festuca sylvatica (woods) | 0·001082 | |
| | | Festuca rubra (turf) | 0·0011 | 0·000407 |
| Galium anglicum (open) | 0·000091 | Galium aparine (scrub) | 0·0227 | 0·022609 |
| Gentiana nivalis (rocks) | 0·000026 | Gentiana anglica (turf) | 0·000128 | 0·000102 |
| Geranium columbinum (open) | 0·0047 | Geranium Phaeum (scrub) | 0·0045 | |
| Geranium molle (arable) | 0·001539 | Geranium pratense (meadows) | 0·00099 | |
| | | Geranium sanguineum (scrub) | 0·0123 | 0·023581 |
| Helianthemum Breweri (open) | 0·000111 | Helianthemum vulgare (turf) | 0·0012 | 0·001089 |
| Hypericum humifusum (open) | 0·00002 | Hypericum androsaemum (woods) | 0·0000625 | 0·000042 |
| Hordeum murinum (open) | 0·0054 | Hordeum sylvaticum (woods) | 0·00757 | 0·00217 |
| Juncus bufonius (open) | 0·000015 | Juncus squarrosus (turf) | 0·0000275 | 0·000012 |
| Lamium amplexicaule (arable) | 0·000526 | Lamium Galeobdolon (woods) | 0·0027 | 0·002174 |
| Lathyrus Aphaca (open) | 0·021 | Lathyrus pratensis (meadows) | 0·0136 | |
| Lathyrus Nissolia (open) | 0·00937 | | | −0·00158 |
| Luzula multiflora (open) | 0·000418 | Luzula Forsteri (woods) | 0·00104 | 0·000622 |
| Medicago minima (open) | 0·000602 | Medicago falcata (turf) | 0·00142 | |

| Species of open or less shaded habitats | Weight in grams | Congeners of more closed and/or shaded habitats | Weight in grams | Difference |
|---|---|---|---|---|
| Medicago minima (open) | | Medicago lupulina (turf) | 0·0012 | 0·000708 |
| Mercurialis annua (arable) | 0·00164 | Mercurialis perennis (woods) | 0·0079 | 0·00634 |
| Phleum arenarium (dunes) | 0·000117 | Phleum pratense (meadows) | 0·000371 | 0·000254 |
| Plantago coronopus (open) | 0·000155 | Plantago lanceolata (meadows) | 0·00155 | 0·001395 |
| Plantago major (open) | 0·0002 | Plantago media (turf) | 0·00079 | 0·00059 |
| Scilla verna (turf) | 0·00156 | Scilla nutans (woods) | 0·006 | 0·00444 |
| Senecio Jacobaea (open) | 0·00028 | Senecio aquaticus (meadows) | 0·00032 | |
| Senecio viscosus (open) | 0·00071 | Senecio erucifolius (turf) | 0·0005 | −0·00002 |
| Senecio vulgaris (open) | 0·0003 | | | |
| Solanum nigrum | 0·000965 | Solanum dulcamara (scrub) | 0·00135 | 0·000385 |
| Sonchus asper (open) | 0·0003 | Sonchus palustris (meadows) | 0·000943 | 0·000583 |
| Sonchus oleraceus (open) | 0·00042 | | | |
| Stachys annua (open) | 0·001075 | Stachys sylvatica (scrub) | 0·0019 | 0·000825 |
| Stellaria media (arable) | 0·000505 | Stellaria Holostea (scrub) | 0·0037 | 0·003195 |
| Trifolium arvense (open) | 0·000122 | Trifolium repens (meadows) | 0·000642 | 0·00052 |
| Trifolium suffocatum (dunes) | 0·000237 | Trifolium pratense (meadows) | 0·0019 | 0·001663 |
| Veronica arvensis (arable) | 0·000122 | Veronica spicata (turf) | 0·00013 | 0·000008 |
| Veronica Buxbaumii (arable) | 0·000926 | Veronica hybrida (scrub) | 0·00018 | −0·000746 |
| Viola tricolor (arable) | 0·0011036 | Viola lutea (turf) | 0·00145 | 0·000346 |
| Total | 0·0758565 | Total | 0·161798 | |
| Average 44 species of more open habitats | 0·001724 | Average 32 species of less open habitats | 0·003852 | Average Difference 0·002128 |

some term such as the product of the average reproductive capacity and the average seed weight. It follows that for the purpose of elucidating other possible correlations the most suitable material is furnished by species having seeds of similar weights and character.

Attention may be called to the fact that there is some evidence that the doubling of the chromosome number in autopolyploids is, in some species at least, accompanied by a parallel increase of the seed weight (*e.g. Pelargonium roseum*, *Solanum lycopersicum*, and *Nicotiana glauca*). From this it would

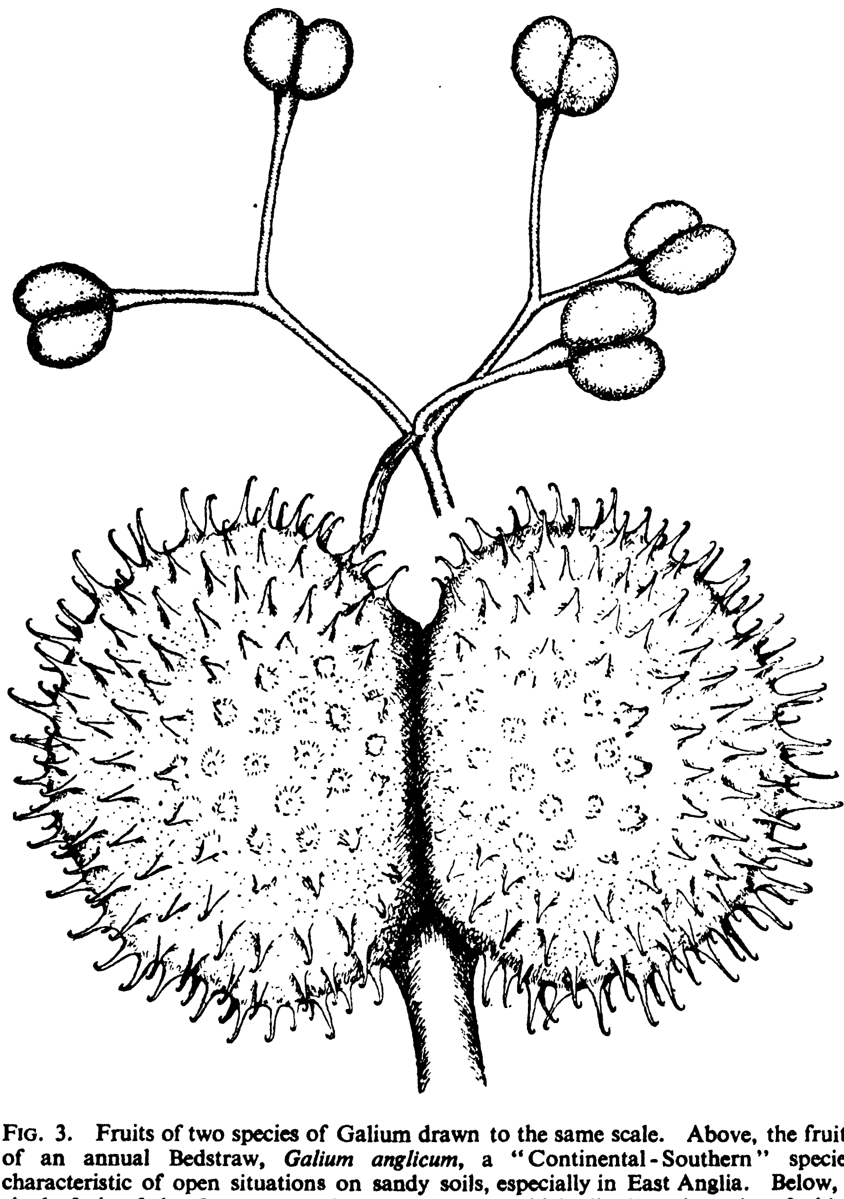


FIG. 3. Fruits of two species of Galium drawn to the same scale. Above, the fruits of an annual Bedstraw, *Galium anglicum*, a "Continental-Southern" species characteristic of open situations on sandy soils, especially in East Anglia. Below, a single fruit of the Goosegrass (*Galium aparine*), a widely distributed species of which the natural habitats are woodland margins and scrub, also their artificial counterparts, hedgerows. The fruits of the scrub species weigh nearly 250 times those of the open habitat species.

then appear that such autopolyploids should be better suited to more advanced communities than their progenitors.

A striking instance is furnished by the segregates of *Phleum pratense* L. studied by J. W. Gregor and F. W. Sansome (1930). These authors distinguished a diploid segregate, with fourteen somatic chromosomes, which is characteristic of well-grazed pastures and short turf, also a hexaploid with forty-two somatic chromosomes, which is typically a plant of meadows rather than of pastures. The " seeds " of the latter segregate have an average weight slightly over one and a half times that of the segregate of the shorter and more open community (*cf.* Fig. 2).

### Variability of Seed Weight

If we accept the conclusion that the possession of a relatively high seed weight confers upon the species the capacity to maintain itself in a more advanced, that is a more closed or taller, community of plants, then also a species in which the variability of seed weight is very marked may, through its occasional production of heavy seeds, however infrequent, be enabled to survive in more advanced communities than would otherwise be possible. That some species exhibit a very small degree of variation in respect to their seed weight is sufficiently evident from the former employment of the grain as a measure of weight. On the other hand, some species show a high degree of variability, which may be exhibited by marked differences between strains or be of a fluctuating character within the strain itself.

Johannes Rafn (*l.c.*) has published data that show the seeds of both the Scots Pine (*Pinus sylvestris*) and the Spruce Fir (*Picea excelsa*) to exhibit an appreciably greater average weight when derived from Mid-European than when derived from Scandinavian sources. (See accompanying Table X.)

TABLE X. WEIGHTS OF 1,000 SEEDS, IN GRAMS. (From J. Rafn.)

| | Minimum | Maximum | Mean | Provenance |
|---|---|---|---|---|
| *Picea excelsa* | 4·10 | 5·16 | 4·47 | Norwegian Northland |
| | 5·07 | 6·02 | 5·60 | Norway and Sweden |
| | 3·97 | 5·5 | 4·97 | Finland |
| | 6·84 | 8·87 | 7·97 | Denmark |
| | 6·73 | 9·68 | 8·06 | Mid-European |
| *Pinus sylvestris* | 3·79 | 5·82 | 4·54 | Finland |
| | 4·75 | 5·41 | 5·15 | Scandinavia |
| | 5·0 | 7·4 | 6·41 | Scottish |
| | 6·0 | 7·5 | 6·65 | Mid-European |

This tendency for the seeds to be heavier the more southerly their provenance is paralleled by the observations of Cieslar that the seeds of forest trees from high elevations are smaller than from lowlands. But, both in respect to latitude and altitude, experimental cultures indicate that we are here dealing with hereditarily different strains rather than with variability within one and the same strain. It is evident that both fluctuating and heritable differences in this respect have a biological significance though not precisely identical.

A considerable range in seed size has been observed by the writer in apparently viable seeds of *Linaria spuria*, but some woodland species are especially noteworthy from this point of view. A particularly striking example is afforded by a sample of seeds of *Convallaria majalis*. Since these were all the produce of clones of the same individual no question can arise of different hereditary strains except for the remote possibility of vegetative mutation. As the range of variation was nearly as great amongst the seeds of one plant as between those of different plants this possibility can be ignored.

The smallest apparently viable seeds were approximately five milligrams in weight, whilst the largest were just over twenty-six milligrams. The standard deviation was 0·0376 gm., with a mean weight of fifteen milligrams. Thus the coefficient of variation was 250 per cent.

Rather less striking were some seeds of *Leucojum aestivum*, of which the largest weighed more than two and a half times the smallest. The average weight of the seeds of *Crataegus monogyna* is higher than that of the seeds of *Crataegus oxycanthoides*, but those of the latter show a greater variability, with a coefficient of variation of 102 per cent, and the average weight of the largest seeds of *C. oxycanthoides* is probably appreciably greater than the corresponding seeds of its congener. Seeds weighing more than a tenth of a gram are not infrequently produced by *C. oxycanthoides* (*ca.* 15 per cent between 0·1 gm. and 0·12 gm.), whilst the smallest are less than 34 milligrams; but its capacity to produce heavy seeds may not be unconnected with its occurrence in rather shadier habitats than *C. monogyna*.

## Heteromorphic Fruits and Seeds

In a certain number of plants there is actual dimorphism or even trimorphism of the seeds or fruits. A striking example of seminal dimorphism is afforded by *Atriplex patula*. Here the majority of the seeds produced by a plant are small (Fig. 4, B), slightly biconvex, black, and shining, and in the seed crops examined comprised about 98 per cent of the total seed output. The diameter ranged from 1 mm. to 1·5 mm. and their average weight was 0·000813 gm.

The larger seeds (Fig. 4, A) are dull brown and flattened, planorbis-like in appearance and constitute between 1 and 2 per cent of the seed crop. Most of these large seeds range in diameter from 1·5 mm. to 2·6 mm. but Hooker (1884, p. 339) gives their maximum diameter as $\frac{1}{6}$ in., or 4·2 mm. The average weight of these larger seeds is about 0·0025 gm. Neither in size nor appearance do there seem to be any intermediates, and the mean weight of the one type is over three times that of the other.

Seeds of the two types, harvested from the same plants as soon as they were ripe and sown immediately, did not germinate till the following spring. The larger seeds germinated first and produced larger and more vigorous seedlings than those from the smaller seeds; but an even more striking distinction was, that during very unfavourable climatic conditions that ensued, all the seedlings derived from the smaller seeds perished, whereas approximately 50 per cent of those derived from the larger seeds survived.

The germination of dimorphic fruits and seeds of a number of species has been studied by Becker (1912), who found generally that *the larger propagules*

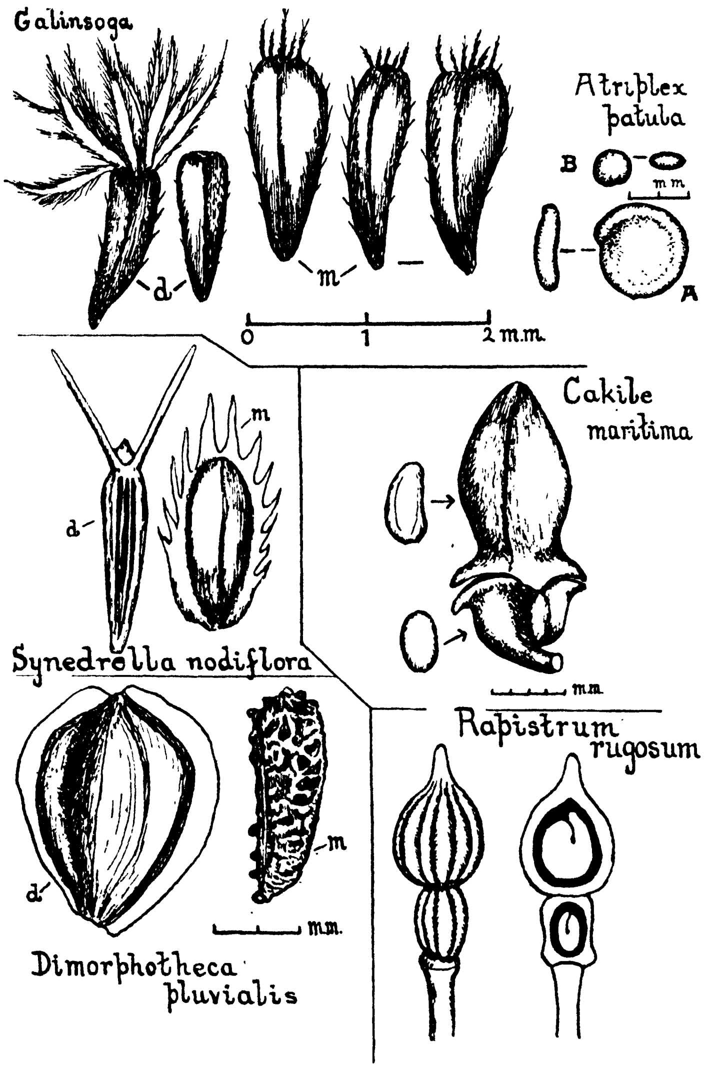



FIG. 4. DIFFERENT TYPES OF SEEDS AND FRUITS PRODUCED BY THE SAME PLANT

*Galingsoga parviflora*, d. disk fruits with and without the pappus. m. marginal fruits from the same capitulum (original). *Atriplex patula*, the two types of seed (A and B) in front view and side view (original). Lower figures after Becker. *Synedrella nodiflora* and *Dimorphotheca pluvialis*, two members of the Compositae showing the disk (d) and marginal (m) fruits. *Cakile maritima* and *Rapistrum rugosum*, two members of the Cruciferae showing the fruits and the dimorphic seeds.

*germinated better and more rapidly than the smaller.* Brief reference may be made to a few of his results.

Amongst the many members of the Compositae which exhibit dimorphic fruits the genus *Dimorphotheca* owes its name to this feature. In *D. hybrida* the central fruits have an average weight of about 0·008219 gm. as compared with 0·011421 gm. for the marginal fruits (ray fruits) of the capitulum. From a number of tests carried out by Becker the average germination of the larger marginal fruits was 79 per cent$\pm$3·3 and of the smaller disk fruits 60 per cent $\pm$4·9. It might be urged that it is the position of the fruits in the capitulum rather than the larger size of the marginal fruits which influences their higher germinating capacity, and therefore another species of the same genus, *D. pluvialis*, in which it is the disk fruits which are the larger (Fig. 4) is instructive. This species formed the subject of investigation by Correns (1906), who found that the disk fruits germinated better and more quickly than the smaller marginal ones, and Becker's experiments confirm this conclusion. In *Gutierrezia gymnospermoides*, where the marginal fruits are also the smaller, there is little difference in the percentage germination, but the marginal fruits germinate much more slowly than the larger disk fruits.

The dimorphic fruits of *Synedrella nodiflora* (Fig. 4) which were previously investigated by Ernst (1906) appear to offer one of the few exceptions to the generalization that the larger fruits germinate better and more quickly. The marginal fruits here have an average weight of 0·000947 gm. and the disk fruits 0·00055 gm. Germination of the latter is slightly higher than of the former, but moreover they germinate more quickly.

In *Galinsoga parviflora* (Fig. 4) the disk fruits are the smaller, and can, like the marginal fruits, yield up to 100 per cent germination; but in eleven tests carried out by Becker under various conditions, some unfavourable, the average germination for the larger fruits was 67·6 per cent$\pm$6 and for the smaller 28·2 per cent$\pm$5·8: a difference of 39·4 per cent, with a probable error of 12·5, so that it may be regarded as markedly significant.

Two cruciferous species in which seeds of two different sizes are produced have been investigated by Becker. The upper seeds of *Rapistrum rugosum* (Fig. 4) are appreciably larger than the lower, and when sown after removal of the fruit wall the larger seeds yielded from 66 to 84 per cent germination as compared with 42 to 46 per cent for the smaller. The upper seeds of *Cakile maritima* (Fig. 4) weigh 0·0093 gm. and the lower 0·00854 gm. The former germinate more quickly, and when freed from the fruit wall yielded 74 per cent germination compared with 70 per cent for the smaller seeds. In both these species fruits sown with the wall intact yielded slightly higher germinations for the smaller seeds.

The experiments upon heteromorphic fruits and seeds indicate quite clearly that, in general, increased size is associated with advantages that would be obviously beneficial under conditions of competition and, it may be emphasized that, differences in size and weight may well have another biological significance as tending to ensure more efficient segregation in their dispersal, thus reducing the stress of intraspecific competition.

Various experiments have been carried out on cultivated plants, in which

small seeds have been compared with large seeds of the same strain and small-seeded strains with large-seeded strains. But in assessing these it must be realized that under the normal conditions of such experiments the factor of competition is reduced to a minimum, so that the benefits of increased food supply for the offspring may be considerably diminished or even obscured.

When B. Szymoniak (1932) carried out experiments with small, medium, and large seeds of seventeen varieties of Pecan, he found no difference in their capacity for germination and little correlation of seed size with growth.

In striking contrast are the results of the experiments carried out by G. R. Eitingen (1926), which are very significant in this connection. He sowed batches of different-sized acorns, of which the average weights were respectively 2·2 gm., 4·7 gm., and 7·2 gm. After five years the heights of the resulting plants were determined, and again after eight years. The average leaf area was also determined. The data are presented graphically in the accompanying Fig. 5. Corresponding with the increasing weight of the acorns from which the sapling oaks were derived they showed an almost parallel increase in their leaf area and an increasing height which is approximately proportional for the Oaks derived from the medium weight acorns; but for those derived from the heaviest acorns the law of diminishing returns would appear to have operated. Since both height and leaf area are important features in relation to competition the significance of seed weight in this connection is obvious.

S. C. Harland (1919), using the small seeds of Sea Island Cotton, found that the small-seeded strains were as vigorous as the large-seeded strains. Nevertheless a comparison of Kohl Rabi and Radish grown from small and large seed, carried out by J. Golinska (1929), showed the advantage of the larger food reserve, notably in the early stages of development. So too some experiments carried out by Vanselow, utilizing small and large seed of Spruce, although indicating no advantage when the site was favourable showed a significantly lower mortality amongst the seedlings raised from the larger seed when the site was an unfavourable one.

That the advantage, under conditions of competition, of a larger food reserve is probably an outcome of the greater capacity for growth is suggested by the experiments of K. Kampe (1929) on Winter Wheat and Rye. This investigator found that when grown from heavier seed the plants produced larger root systems. Better root development from heavy seed has also been noted in other plants.

Variability of seed size in the same species or strain may be an hereditary character, but it is also largely influenced by the competition for food between the flowers of the same individual or even between the seeds in the same fruit. The former condition explains the fact that in the Rice plant Y. Yamaguchi (1919) found that there was a correlation between seed weight and position of the flower in the panicle. The heaviest seeds were usually those produced by the 3rd to the 6th flowers from the apex and were generally from those flowers which were the first to open. This suggests that priority in the competition for nutrients was involved. In this connection the results obtained by C. A. Crandall (1918) are of interest. He found that the seedlings raised from apple pips derived from the larger fruits on the tree were more resistant

to adverse conditions than seedlings which had been raised from pips derived from the smaller fruits of the same parent.

The relation between seed weight and number is subject to marked variation. Sometimes there is a negative correlation between seed weight and number and sometimes a positive one. This apparent divergence is the outcome of two conflicting influences. One, the nutrition of the plant, tends to increase not only the number of fruits but also the number and size of the seeds which

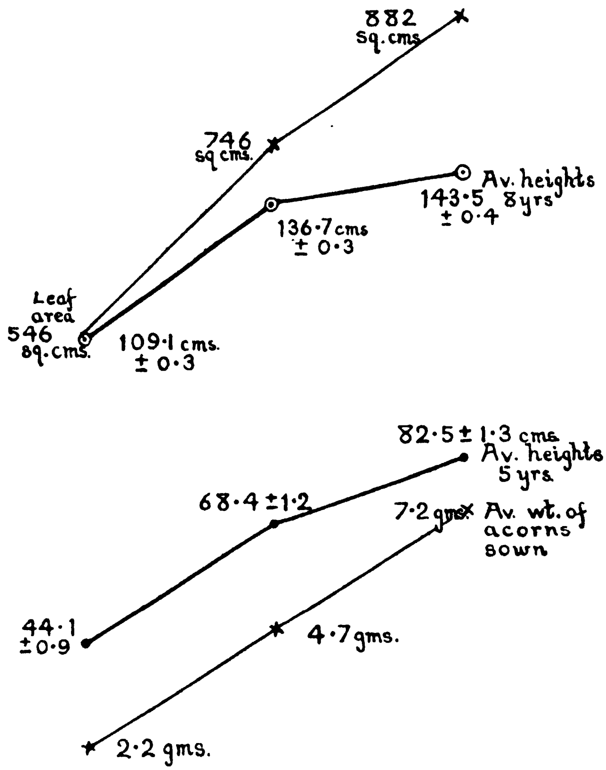



FIG. 5. Diagram showing relation between weight of Acorns and the growth of the saplings they produce. The average heights of the saplings after five years' growth and after eight years is shown and also their average leaf area. (From Eitingen's data.)

they contain. Thus, if nutrition conditions be very favourable both during the flowering period and throughout fruit development number and size alike tend to be augmented. Under less favourable conditions of nutrition, especially if they tend to decline during the later phases of reproduction, the competition between the developing seeds for food material may lead to a negative correlation between their number and weight. Critical phases such as flower formation, ovular development, pollination, fertilization, etc., will obviously affect this competition, but even despite the complex of internal and external factors involved most species exhibit a low variability of seed weight whilst in others the variability is appreciable.

Data respecting the seed weights of *Albizzia Lebbek*, from pods containing from one to twelve seeds, were obtained by Guppy (1912), and though the range of variation amounts to only about 13 per cent, yet calculation of the correlation coefficient from Guppy's data shows that there is a marked negative correlation between seed weight and the number of seeds in the pod ($r = -0{\cdot}569$). His data for *Iris pseudacorus* and *Iris foetidissima* are relatively few but show a marked positive correlation. Judging by the results obtained by G. Vincent (1939) from observations on Conifers, these would appear to show a positive correlation between seed number and size, for this investigator found that large cones generally contained larger and more numerous seeds. But though certain species will be more prone to exhibit a positive and others a negative correlation, yet, having regard to the more obvious factors involved, it would seem unlikely that there should be constancy in this respect under all conditions of nutrition or other variations of the environmental factors.

In general, though some species are prone to exhibit marked variations in seed weight, of which examples have already been cited, yet favourable or unfavourable environmental conditions affect seed number more than seed size, so that depauperate plants tend to produce a few seeds of more or less normal weight rather than a larger number of seeds of diminished size. In evaluating seed output it is thus of considerable importance to know whether the seeds produced by the less vigorous individuals are equally viable and produce plants of equal vigour as those which are the produce of more robust individuals. Experimental evidence in this connection will be dealt with in the next section.

Not only may different strains of the same species differ with respect to the mode of their seed weight but the same strain may yield heavier seed when cross-pollinated than when selfed. Thus cross-pollination in Maize was found by D. F. Jones (1918) to yield " seeds " that exhibited an average increase of weight, compared with those produced by self-pollination, of from 5 to 35 per cent. The findings of T. Ishii (1930) that in the genus *Dianthus* the average size and weight of the seeds varies with the number or volume of the chromosomes is probably an expression of the same phenomenon as the increase in size of parts that tetraploids show compared with diploids. H. W. Howard (1939) found that the seeds of tetraploid *Brassica oleracea* weigh about 1·3 times as much as the seeds of diploid plants of the same species.

A striking example of the influence of hybridization on seed weight is afforded by the experiments of J. W. McKay and H. L. Crane on the Sweet Chestnut (*Castanea*). These investigators found a difference in mean seed weight according to the species of male parent employed which amounted to 8·4 gm. This was four-and-a-half times the standard error (McKay and Crane, 1938).

We may also recall the observations of Darwin (1880) that the seed weight of the three types of Purple Loostrife (*Lythrum salicaria*), like the size of their pollen grains, diminishes in correspondence with the lengths of their styles. Thus he found that 100 seeds of the plants with long styles were equal in weight to 121 seeds of plants with styles of medium length and to

142 seeds of short-styled plants. It is worthy of note that the average number of seeds per capsule which he recorded for the three types were 93, 130, and 83 respectively, so that there is apparently no relation between the weight of the seeds and the number in the capsule. The differences in seed weight between the three types would tend to segregate them when dispersed by wind action, a feature that is somewhat surprising in view of the low seed production which self-fertilization brings about.

Addendum re. seed weights.

Averages based upon a large number of seeds were not available for the Sea Convolvulus and the Sea Pea, but the weights of a small number have been determined as follows:

Sea Pea, *Lathyrus maritimus* (L.) Bigel. (Average of ten seeds) 0·023 gm. per seed.

Sea Convolvulus, *Convolvulus Soldanella* L. (Average of 31 seeds) 0·0568 gm. per seed.

The one is a colonizer of bare shingle and the other of early phases in the dune succession. By contrast we may note that the dune vetch, *Vicia lathyroides* L. which is a species of bare areas on dunes in the later stages of development, has seeds which weigh 0·00238 gm. (average of 252 seeds), and this may be compared with 0·0182 gm. for the average weight of the seeds of its closely allied congener of pastures *Vicia angustifolia*.

*Filago germanica* L. Sixteen hundred seeds of this Cudweed weighed 0·0496 gm., or an average of 0·000031 gm. per seed. It is a species of bare areas on old dunes and dry banks.

Other open habitat species.

Ground Pine, *Ajuga chamaepitys* (L.) Schreb., a plant of bare places on chalky soil. The average weight of the nutlets is 0·00116 gm.

*Teucrium Botrys* L. A biennial exhibiting marked fluctuations in numbers and confined to open situations on chalky soils. The average weight per nutlet of 178 nutlets was 0·00123 gm.

Proliferous Pink, *Dianthus prolifer* L. The average weight per seed (average of 853 seeds) was 0·00258 gm.

Rock Stonecrop, *Sedum rupestre* L. Average weight per seed (917 seeds) 0·000054 gm.

*Cynoglossum officinale* (L.) Dunes. 0·032 gm.

*Seseli Libanotis* Koch. 0·00169 gm.

Marsh and meadow.

*Cicuta virosa* L. 0·00168 gm.
*Eupatorium cannabinum* L. 0·000416 gm.
*Peucedanum palustre* Moench. 0·00371 gm.
*Thalictrum collinum* Wallr. 0·0031 gm.

Woodland.

*Inula Conyza* DC. 0·00017 gm. (clearings).
*Pyrola uniflora* L. 0·000004 gm.

Shrubs.

*Daphne laureola* L. 0·0242 gm.
*Ligustrum vulgare* L. 0·0077 gm.

# III

# THE VIABILITY OF SEEDS FROM PLANTS OF DIVERSE VIGOUR

In any attempt to estimate the average reproductive capacity of a species it is manifestly of great importance to know whether the produce of individuals of different vigour is merely quantitatively different or qualitatively distinct also. In view of the fundamental nature of this question a number of experiments have been carried out with the assistance of Miss Edith M. Cooper, B.Sc., and Miss M. Lawford, B.Sc., for whose help I am much indebted.

For the purpose of this inquiry the vigour of the parent plant has been assumed to be proportional to the number of fruits which it bears, a criterion that would appear to be a valid measure of vigour in the species selected, and has moreover the advantage of simple numerical assessment. Three monocarpic species were chosen, viz. *Silene quinquevulnera*, *Silene conica*, and *Solanum nigrum*. For each of these, seeds were collected from plants with a known number of fruits. For the first two species seeds were obtained from a considerable number of different individuals in each fruit-production category, so that the tests were carried out on samples obtained from the mixing together of the seeds of all the individuals which bore the same number of fruits. For *Solanum nigrum* the seeds were obtained from a single individual of each category.

### *Silene quinquevulnera*

Seeds were obtained of this species from plants bearing from one to 327 capsules. Samples of 100 seeds each were sown under uniform conditions.

TABLE XI. PERCENTAGE GERMINATION OF SEEDS OF *SILENE QUINQUEVULNERA* FROM PARENTS OF DIVERSE VIGOUR AS INDICATED BY THE NUMBER OF CAPSULES THEY BORE

(I) Seeds of 1930

| | Number of capsules borne by parents | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 10 | 15 | 20 | 22 | 39 | 63 | 116 | 163 | 327 |
| Planted 15/10/30 | 86 | 83 | 82 | 92 | 64 | 93 | 99 | 44 | 92 | 99 |
| 27/10/30 | 74 | | 73 | 91 | 56 | 85 | 96 | 39 | 95 | 99 |
| 4/11/30 | 57 | | 79 | 84 | 43 | 94 | 92 | 51 | 84 | 99 |
| 12/1/31 | | | 72 | 81 | 39 | 84 | 98 | 20 | 89 | 100 |
| 12/1/31 | | | 76 | | | | | 18 | 92 | 100 |
| 23/2/31 | | | 77 | | | | 93 | 27 | 84 | 100 |
| 11/5/31 | | | | | | | 90 | 4 | 90 | 100 |
| 21/12/31 | | | 50 | | | 75 | 67 | | 81 | 100 |
| Average of all sets | 72 | 83 | 73 | 87 | 50·5 | 86 | 91 | 29 | 88 | 100 |

(II) Seeds of 1931

| | Number of capsules borne by parents | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 42 | 11 | 12 | 14 | 20 | 26 | 31 | 35 | 53 | 60 | 91 | 115 | 204 |
| Planted 21/12/31 | | 92 | | 92 | | | | | | | | 86 | | 100 |
| 15/1/32 | 100 | | 100 | | 100 | 88 | 95 | 94 | 97 | 100 | 100 | 88 | 100 | 100 |

Seventy samples were altogether tested, of which 54 were of seed collected in 1930 and 16 of samples obtained in 1931; a total of 7,000 seeds for the two years together. The results of the germination tests are furnished in Table XI.

The average percentage germination for this species is 80 per cent (79·7 per cent). If the percentage germinations are plotted against the number of capsules borne on the parent it is at once obvious that no correlation is exhibited between parental vigour as measured in this way and the germinative capacity of the seeds.

Treating each sample of 100 seeds as a single observation and grouping them together in classes of approximately equal size, the statistical constants are as follows:

| Seeds from plants bearing from 1 to 21 capsules: | Seeds from plants bearing from 22 to 91 capsules: | Seeds from plants bearing from 115 to 327 capsules: |
|---|---|---|
| Mean germination 82 per cent | Mean germination 84 per cent | Mean germination 77 per cent |
| Standard deviation =9·06 | $\sigma$=17·0 | $\sigma$=30·75 |
| Standard error of mean 2·01 | S.E.M. 3·54 | S.E.M. 6·03 |

| Differences of means | | Standard errors of differences |
|---|---|---|
| B–A | 2 | 4·07 |
| A–C | 5 | 6·35 |
| B–C | 7 | 6·99 |

It is clear from these data that the differences of the means are not significant.

Though it be true that the percentage germinations of seeds from the plants with a very large number of capsules in 1930 was rather more uniformly high, yet of the 1931 seeds those from plants with 2, eleven, and 14 capsules respectively showed 100 per cent germination equally with the seeds of plants bearing 53, 60, 115, and 204 capsules.

Similar results were obtained with *Silene conica*, where, as shown in Table XII, the average percentage germination was not significantly different whether the parent individual was a large plant bearing 73 capsules or a very depauperate plant bearing only one.

TABLE XII. PARENTAL VIGOUR AND PERCENTAGE GERMINATION OF *SILENE CONICA*

| | | Number of capsules borne by parent | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | 4 | 6 | 21 | 55 | 73 |
| Date of sowing | 3/11/30 | 99 | 100 | 100 | 97 | 100 | 91 |
| ,, ,, | 3/11/30 | 100 | 99 | 100 | 97 | 100 | 96 |
| ,, ,, | 21/1/31 | 99 | 100 | 100 | 94 | 99 | 97 |
| ,, ,, | 23/1/31 | 100 | 100 | 100 | 96 | 99·9 | 94·8 |
| Average percentage | | 99·5 | 99·8 | 100 | 96 | 99·8 | 94·8 |

The mean value is here 98·2 per cent. Only forty-two of the 2,400 seeds sown failed to germinate. Here, actually, it was the seeds of the most vigorous plants which yielded the lowest average germination, but the differences are again too slight for any importance to be attached to them.

The results for *Solanum nigrum*, a monocarpic species of quite a different character, indicate the same conclusion (*cf.* Table XIII).

TABLE XIII. PARENTAL VIGOUR AND GERMINATION IN BLACK NIGHTSHADE, *SOLANUM NIGRUM*

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of berries on parent | 69 | 81 | 85 | 87 | 103 | 128 | 136 | 162 | 168 | 219 | 223 | 259 | 335 | 576 |
| Percentage germination | 99 | 100 | 85 | 94 | 100 | 100 | 99 | 99 | 98 | 100 | 100 | 97 | 100 | 98 |

It is quite evident, therefore, that so far as these species are concerned there would appear to be no difference in the germinative capacity whether the seeds be derived from larger plants or depauperate ones, and casual tests with seeds from large and very small plants of other species indicate that this is probably true generally.

In addition to testing for germination capacity the cultures of these three species were examined also with respect to the number of apparently healthy plants, and the mortality rates were studied. Thus an estimate was obtained of the relative quality, as well as the quantity, of seedlings produced.

TABLE XIV. *SILENE QUINQUEVULNERA*. PERCENTAGE OF HEALTHY PLANTS IN EARLY PART OF EXPERIMENT AND PERCENTAGE MORTALITY AT END

| 1930 | Number of capsules on parent | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 15 | 20 | 22 | 39 | 63 | 116 | 163 | 327 |
| Percentage healthy plants— | | | | | | | | | |
| Average | 50·5 | 68 | 79 | 40 | 84 | 89 | 23·5 | 82 | 99·6 |
| Maximum | 61 | 73 | 85 | 52 | 90 | 94 | 45 | 91 | 100 |
| Average percentage mortality | 23·7 | 9·2 | 7·9 | 13·8 | 4·1 | 5·9 | 16·7 | 7·1 | 0· |

| 1931 | Number of capsules on parent | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 11 | 14 | 20 | 26 | 31 | 35 | 53 | 60 | 91 | 115 | 204 |
| Percentage healthy plants | 100 | 95 | 97 | 79 | 95 | 91 | 95 | 100 | 100 | 85 | 97 | 100 |
| Percentage mortality | 0 | 4 | 3·1 | 10 | 0 | 3·2 | 2 | 0 | 0 | 4·5 | 3 | 0· |

These data for *Silene quinquevulnera* seed collected in 1930 suggest a greater vigour of the seedlings derived from the largest parents, especially when compared with those derived from seeds of plants bearing only one capsule, but the plants of intermediate size show no gradation of either mortality or the proportion of healthy plants amongst their offspring such as we might expect if the contrast between the two extremes was significant. On the other hand the data from the seed collected in 1931 show no such contrast between the extremes, and indeed no indication whatever of any difference in vigour of the offspring, related to the size of the parents.

The corresponding data for *Silene conica*, Table XV, and Black Nightshade, *Solanum nigrum*, Table XVI, tend to confirm the conclusions based on *S. quinquevulnera*.

The conclusion seems warranted, therefore, that though a vigorous plant may produce seeds which by virtue of their slightly larger size yield seedlings that exhibit a greater vigour, yet, in general, the effect of adverse conditions upon fruiting individuals is to diminish the number of seeds produced, but normally has little, if any, effect upon their quality. It is as though, in the matter of seed production, the plant obeyed a sort of "quantum law," and

TABLE XV. *SILENE CONICA*. PERCENTAGE OF HEALTHY PLANTS IN EARLY PART OF EXPERIMENT AND OF MORTALITY AT END

| | Number of capsules on parent | | | | | |
|---|---|---|---|---|---|---|
| | 1 | 4 | 6 | 21 | 55 | 73 |
| Percentage healthy plants— | | | | | | |
| Average | 92 | 91·2 | 93·2 | 88·5 | 95·2 | 89·5 |
| Maximum | 100 | 100 | 100 | 97 | 100 | 96 |
| Percentage mortality— | | | | | | |
| Average | 8 | 7·5 | 6·5 | 8·5 | 4·2 | 6·6 |
| Maximum | 18 | 28 | 25 | 21·9 | 16 | 13·4 |

TABLE XVI. BLACK NIGHTSHADE, *SOLANUM NIGRUM*. PERCENTAGE OF HEALTHY PLANTS IN EARLY PART OF EXPERIMENT AND MORTALITY AT END

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of berries | 69 | 81 | 85 | 87 | 103 | 128 | 136 | 162 | 168 | 219 | 223 | 259 | 335 | 576 |
| Percentage healthy plants | 95 | 84 | 79 | 88 | 98 | 100 | 90 | 97 | 96 | 87 | 100 | 91 | 87 | 83 |
| Percentage mortality | 4·2 | 19 | 7·6 | 6·8 | 2 | 0 | 10 | 2 | 2 | 15 | 0 | 6·6 | 12·6 | 18·1 |

that below a certain minimum food supply the ovule or seed normally aborts. In estimating average seed production we shall then be justified in regarding the seeds produced by small individuals as qualitatively comparable with those produced by large individuals. This is particularly important in respect to some monocarpic species, which not uncommonly occur in fluctuating numbers: in some seasons as a comparatively small number of scattered and large individuals, in others as multitudes of crowded and depauperate plants. If, to the difference in size of seed output, were added the complication of a difference in quality also the difficulty of our problem would have been considerably enhanced.

With respect to the effect of space upon seed yield the law of diminishing returns also applies. H. A. Jones and S. L. Emsweller (1939) found that the seed yield of onions spaced at distances of 3, 4, 6, 8, and 12 in. respectively increased with the distance between the plants but there was a corresponding decrease in the yield per acre. Clements *et al.* (1929) grew *Helianthus annus* under carefully controlled conditions at distances of 2, 4, 8, 16, 32, and 64 in. apart, and the resultant yields, of seed in weight per unit area, were 480, 1,424, 1,896, 2,028, 1,880, and 1,803. Thus, for spacing between 8 in. and 64 in. there was no significant difference in yield. Kiesselbach's experiments with from one to five plants of Maize per hillock showed a wide range in the yield per plant but little difference in yield per unit area whether the plants were two, three, four, or five per hillock. With but a single plant the yield per acre was slightly lower.

There is, in fact, probably for each species a wide range of density over which the productivity remains fairly constant, the magnitude of the lower and upper limits of this range of spacing depending to a considerable extent upon the size and habit of the plant. Below a certain specific density increasing yield of the individual fails to compensate for the diminished population.

On the other hand, above a certain density the individuals become so depauperate through competition, from germination onwards, for essential requirements that the augmented population fails to compensate for the low yield of each individual. It is probable, therefore, that when we are concerned with relatively pure stands, whether such social species be the outcome of reproduction by seed or of vegetative propagation, the yield per unit area is a more satisfactory basis for comparison than the yield per plant. For comparison with non-social species, however, the yield of individuals in sparse communities offers perhaps the most useful basis.

# IV

## METHODS AND TERMINOLOGY

The seed production of plants can in some instances, where the number is not too great, be determined directly by actual counts of the seed produced; but usually it is necessary to resort to some type of estimation, since the exact determination of the number of seeds produced by a few individuals is less important than an approximation to the seed production of many. Attempts to avoid this difficulty by determining the seeds produced by an assumed average individual are liable to grave error, as the "average individual" is only satisfactorily estimated after a considerable number have been examined. The source of error, unless this is done, is often considerable, since one's judgment is biased by size, and insufficient weight is given to the perhaps numerous individuals with few fruits. Moreover, the individuals of many species, particularly, but by no means exclusively, those which are monocarpic, tend to consist of a small proportion which are relatively large and a large proportion of small individuals. Under such circumstances the "average" individual may not exist in fact, but is an abstraction and can only be ascertained by "random sampling."

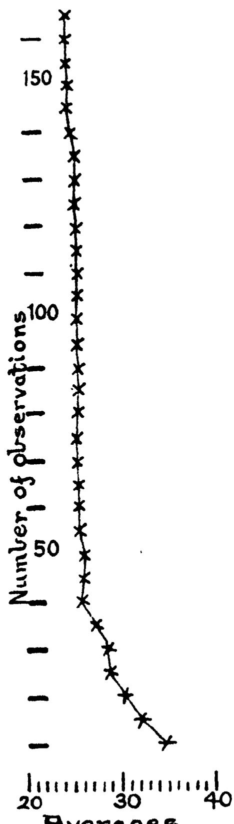



FIG. 6. Diagram showing the change in the mean number of seeds per capsule of The Corn Cockle (*Agrostemma Githago*) with increments of five capsules in the number in which the seeds were counted. The mean for ten capsules was 34·8, for thirty capsules 28·56, for forty capsules 25·9, for one hundred capsules 25·5, and for one hundred and sixty-five capsules 24·5.

Despite the great labour involved, it is essential, if the data are to have any permanent value, that they should be based on careful estimates of the species in its *normal* habitat with due regard to the range of variation there exhibited.

The first question that naturally arises is the number of individuals that must be examined to obtain a more or less reliable estimate. Determinations of the probable error of the mean of any set of observations occupies a considerable time, which, in the field, where the material is available could often be better spent in acquiring more data. An empirical method has therefore been adopted which involves a minimum of time spent on arithmetical calculation in the field.

According to the magnitude of the figures involved and the degree of dispersion an arbitrary number of specimens are counted and the mean value determined. Further batches are then counted and the mean reassessed until the mean remains reasonably constant with each further addition of data. Often, however, the data are limited by either the time factor or by the

number of specimens available. The empirical method is illustrated for the number of seeds per capsule of *Agrostemma Githago* in Fig. 6, showing the varying mean with increments of five capsules.

In those species whose fruits contain more than one seed the mean value for both the number of seeds per fruit and the number of fruits per plant has been determined. The mean of the products, of these two mean values, plus or minus their probable errors, gives us what we shall term the *Average Seed Output*. In a considerable number of instances amongst the species investigated the average percentage germination of the seeds has been determined. The product of the average seed output and the fraction represented by the average percentage germination gives us what may be termed the *Average Reproductive Capacity*. This term should also include an estimate of the rate of vegetative multiplication, where this is a significant feature. But for brevity of expression the term when used without qualification in this work may be understood to refer to reproduction by seed alone.

The product of the average seed output and of the average weight of a seed may be termed the *Average Output Weight*, whilst the product of the average weight of a seed and the average reproductive capacity furnishes the *Average Reproductive Weight*.

# V

# THE INFLUENCE OF SOIL AND CLIMATIC CONDITIONS ON SEED OUTPUT

It is a familiar fact that the range in plant size, and with this the " Seed Output," is often very considerable, and it will be necessary to estimate the effect of habitat conditions upon this feature; but, for the moment, it may be well to emphasize the importance of distinguishing between the potential capacity of a species when grown in the most favourable conditions and the output which it exhibits in the habitat conditions where it naturally occurs. The latter can alone furnish us with evidence of any correlation between the occurrence of a species and its reproductive capacity.

In view of the importance of this distinction between natural and artificial habitats one or two examples of the differences which obtain may be cited.

*Dianthus prolifer* is, in Britain, a very infrequent annual of dry, gravelly pastures where it is not uncommonly very depauperate. These depauperate plants may bear only a single flower, and specimens were found in which the entire plant was only 5–6 cm. high and produced only eight seeds. But plants raised from these seeds in cultivated ground, practically free from competition, were richly branched, and some attained a height of 90 cm. One such specimen bore 205 capsules, with an average of 34 seeds in each; a total seed output of some 6,970 seeds. *Ranunculus parviflorus* is also an annual of dry, shallow soils and sand dunes, where the number of achenes produced by a plant commonly ranges from 54, or fewer, to about two hundred and fifty. In cultivated ground, however, the number of achenes per plant may attain to over two thousand. As this species not only occurs in the natural habitats mentioned but also as a weed of cultivated ground its potentialities in this environment are of biological significance.

The influence of soil conditions is illustrated by *Cardamine hirsuta*. This species most frequently occurs as a weed of cultivated soil but is also found as a member of the annual flora of young dunes. Specimens were collected from the dunes at Harlech and also from clay soil on the top of a wall bordering the dunes. Both sets thus had much the same climatic conditions; they were alike well-drained; but the one set grew on a soil retentive of moisture and the other in a dune soil where the water content varied between 1 and 4 per cent. It will be seen that the average number of capsules on the plants growing on clay soil is rather more than four times the average for the dune plants. The actual difference is 20·25 siliquas, and the standard error of the difference 4·25. The difference in number of fruits is thus quite significant. It may be added that on well-manured cultivated soil adjacent to the wall an exceptionally large plant, more or less free from competition, was examined which had 1,676 siliquas!

The number of seeds per pod of the dune plants ranged from 14 to 24, with an average of 17·45 seeds (standard deviation 1·93; standard error of mean

TABLE XVII. NUMBER OF SILIQUAS ON PLANTS OF HAIRY CRESS, *CARDAMINE HIRSUTA*, IN CLAY AND SAND

| No. of siliquas | Dunes | Clay | No. of siliquas | Dunes | Clay | No. of siliquas | Dunes | Clay |
|---|---|---|---|---|---|---|---|---|
| 1 | 8 | 0 | 19 | 0 | 1 | 37 | | 1 |
| 2 | 15 | 0 | 20 | 0 | 2 | 38 | | 0 |
| 3 | 25 | 4 | 21 | 0 | 2 | 39 | | 1 |
| 4 | 15 | 5 | 22 | 1 | 3 | 43 | | 2 |
| 5 | 13 | 5 | 23 | 1 | 0 | 45 | | 1 |
| 6 | 13 | 7 | 24 | 1 | 1 | 49 | | 1 |
| 7 | 9 | 6 | 25 | 1 | 1 | 64 | | 2 |
| 8 | 5 | 3 | 26 | 0 | 1 | 75 | | 1 |
| 9 | 6 | 6 | 27 | 0 | 1 | 83 | | 1 |
| 10 | 2 | 8 | 28 | 1 | 0 | 89 | | 1 |
| 11 | 2 | 1 | 29 | | 1 | 95 | | 1 |
| 12 | 2 | 6 | 30 | | 2 | 100 | | 1 |
| 13 | 2 | 2 | 31 | | 1 | 121 | | 1 |
| 14 | 0 | 2 | 32 | | 1 | 128 | | 1 |
| 15 | 0 | 2 | 33 | | 2 | 134 | | 1 |
| 16 | 0 | 0 | 34 | | 1 | 145 | | 1 |
| 17 | 0 | 1 | 35 | | 1 | 171 | | 1 |
| 18 | 0 | 1 | 36 | | 1 | | | |

| | | | |
|---|---|---|---|
| Total dune plants | 122 | Total plants on clay | 99 |
| Average number of siliquas (per plant) | 5·63 | Average number of siliquas | 25·88 |
| Standard deviation | 4·74 | Standard deviation | 33·3 |
| Standard error of mean | 0·43 | Standard error of mean | 3·33 |

0·41). The plants on clay had from 18 to 30 seeds per pod (standard deviation 2·45; standard error of mean 0·32). The difference of the means for number of seeds per pod was thus 7·28 seeds, and the standard error of the difference 0·52. The effect of the more favourable soil conditions is thus to increase both the number of fruits and the number of seeds which they contain. The superabundance of this species in some gardens can doubtless in part be attributed to the response of its seed output to the favourable conditions, just as its comparative subordination in the annual flora of the dune can perhaps be partly related to the much lower output it achieves under these conditions (*ca.* 98 seeds per plant). On the clay soil the average seed output is 640 seeds per plant, whilst the seed production of the luxuriant plant referred to, which had an average of 31 seeds per pod, must have been nearly fifty-two thousand! It will be noted that with increasing favourability of the habitat conditions there was an increase in number of seeds per pod as well as of the number of pods per plant.

With the object of ascertaining the effect of various edaphic and climatic conditions upon the number of seeds in the capsule, *Anagallis arvensis* was selected as being a species that had a wide range and could be obtained from conditions of comparable character as regards competition, since, as will be shown later, this is an important factor in seed production. Further, in addition to its occurrence in cultivated ground, *A. arvensis* also occurs on dunes where the degree of competition is similar. I have elsewhere shown that the dune is about half as favourable as cultivated ground for this species with respect to water supply, as indicated by the use of the stomatal frequency

as an integrating index of the water relations of the plant (*cf.* Salisbury, E. J., 1932), the mean stomatal frequencies being respectively 63·5 and 132·3.

The number of capsules per plant exhibits a wide range under these different conditions of climate and soil, and it is evident that if the range in number of seeds per capsule is comparable to the range in size of the plants a very

TABLE XVIII. SCARLET PIMPERNEL, *ANAGALLIS ARVENSIS*. NUMBERS OF SEEDS PER CAPSULE FROM VARIOUS LOCALITIES. (All arable except Dunes, Norfolk.)

| No. of seeds per capsule | | Norfolk (Dunes) | Slough, Bucks. | Radlett, Herts. | Letchworth, Herts. | Stowmarket, Suffolk | Melton, Norfolk | Guernsey | Sark |
|---|---|---|---|---|---|---|---|---|---|
| 0 | Tot (11) | 2 | 3 | 0 | 1 | 2 | 3 | 0 | 0 |
| 1 | (6) | 0 | 0 | 0 | 1 | 0 | 1 | 4 | 0 |
| 2 | (7) | 1 | 0 | 0 | 0 | 2 | 3 | 0 | 1 |
| 3 | (10) | 2 | 1 | 0 | 3 | 1 | 2 | 0 | 1 |
| 4 | (28) | 3 | 1 | 1 | 2 | 3 | 12 | 3 | 3 |
| 5 | (28) | 6 | 0 | 1 | 3 | 8 | 7 | 1 | 2 |
| 6 | (49) | 7 | 2 | 2 | 6 | 10 | 14 | 3 | 5 |
| 7 | (46) | 7 | 3 | 2 | 2 | 12 | 12 | 4 | 4 |
| 8 | (56) | 4 | 5 | 2 | 4 | 14 | 19 | 3 | 5 |
| 9 | (66) | 12 | 2 | 5 | 3 | 14 | 17 | 2 | 11 |
| 10 | (81) | 13 | 2 | 2 | 8 | 18 | 23 | 7 | 8 |
| 11 | (111) | 18 | 4 | 4 | 5 | 26 | 29 | 11 | 14 |
| 12 | (127) | 31 | 3 | 5 | 5 | 29 | 29 | 7 | 18 |
| 13 | (155) | 30 | 8 | 5 | 9 | 29 | 29 | 15 | 30 |
| 14 | (180) | 31 | 8 | 6 | 15 | 34 | 27 | 25 | 34 |
| 15 | (172) | 21 | 6 | 8 | 4 | 32 | 39 | 23 | 39 |
| 16 | (168) | 18 | 8 | 13 | 13 | 31 | 20 | 30 | 35 |
| 17 | (150) | 11 | 4 | 9 | 6 | 33 | 18 | 36 | 33 |
| 18 | (167) | 9 | 10 | 18 | 6 | 20 | 24 | 34 | 46 |
| 19 | (182) | 8 | 11 | 10 | 6 | 32 | 21 | 45 | 49 |
| 20 | (179) | 2 | 13 | 24 | 8 | 21 | 17 | 57 | 37 |
| 21 | (204) | 4 | 10 | 21 | 9 | 23 | 13 | 72 | 52 |
| 22 | (177) | 0 | 10 | 18 | 6 | 19 | 8 | 75 | 41 |
| 23 | (143) | 1 | 12 | 10 | 4 | 6 | 1 | 70 | 39 |
| 24 | (129) | | 4 | 8 | 5 | 10 | 2 | 75 | 25 |
| 25 | (127) | | 7 | 15 | 4 | 5 | 6 | 67 | 23 |
| 26 | (96) | | 7 | 8 | 0 | 5 | 2 | 53 | 21 |
| 27 | (73) | | 4 | 6 | 3 | 4 | 4 | 37 | 15 |
| 28 | (46) | | 3 | 3 | 1 | 2 | 1 | 22 | 14 |
| 29 | (37) | | 1 | 2 | 1 | 0 | 0 | 26 | 8 |
| 30 | (30) | | 4 | 2 | 0 | 0 | 0 | 15 | 8 |
| 31 | (20) | | 0 | | 0 | 1 | 0 | 10 | 9 |
| 32 | (15) | | 3 | | 0 | | | 9 | 3 |
| 33 | (7) | | 1 | | 0 | | | 5 | 1 |
| 34 | (8) | | 2 | | 0 | | | 2 | 4 |
| 35 | (4) | | 0 | | 0 | | | 2 | 2 |
| 36 | (7) | | 1 | | 1 | | | 3 | 2 |
| 37 | (2) | | | | | | | 1 | 1 |
| 38 | (1) | | | | | | | | 1 |
| **Totals** | | 241 | 163 | 210 | 144 | 446 | 403 | 854 | 644 |

**3,105 capsules. Arithmetic mean 18 (17·86) seeds per capsule. Standard error of mean 0·11**

large number of determinations would be necessary to obtain a satisfactory average.

I am indebted to members of my Department for assistance in determining the number of seeds per capsule of plants growing on the dunes at Blakeney Point; to Miss R. Dowling, M.Sc., for the data from arable land near Slough; to Mr. H. Thompson, B.Sc., who has examined 446 capsules from sandy-loam at Stowmarket, Suffolk, 144 from similar soil at Letchworth, Herts., and 845 capsules from Guernsey and 644 from Sark; also to Miss E. Rowe, M.Sc., for examining 400 capsules from plants at Melton Constable, Norfolk. The data thus comprise counts from over three thousand capsules, and involved the counting, under a lens, of over 55,000 seeds. It is this great labour involved which is doubtless responsible for the extreme neglect from which the problems with which we are concerned have suffered, despite their great biological importance.

For all the capsules examined (3,105) the average number of seeds is 18 (17·86)$\pm$0·07, and for the individual localities the average ranges from 12·68 for the dune plants to 21·63 for those from arable land in Guernsey. The standard deviation is of the same order of value in most habitats, the exceptions being for the dune plants and those from dry, sandy loam over gravel at Radlett, Herts.

It is evident from the statistical data furnished in Table XVIII and the accompanying graph (Fig. 7) that the range of variation is very similar for most habitats, except for the dunes.

In Table XIX the means for the various stations and the statistical constants are furnished, and it is evident that some of the differences of means are significant; but if we take the extreme values represented by the dune plants and those from Guernsey the difference expressed as a percentage of

TABLE XIX. STATISTICAL DATA. SEEDS PER CAPSULE SCARLET PIMPERNEL, *ANAGALLIS ARVENSIS*

| Locality | Arithmetic mean of seed number per capsule | Standard deviation | Standard error of mean | Coefficient of variation | Rain in inches |
|---|---|---|---|---|---|
| All habitats | 18(17·88) | 6·41 | 0·11 | 35·8% | |
| Dunes, Blakeney | 13(12·68) | 3·79 | 0·24 | 29·6% | *ca.* 22 |
| Melton, Norfolk | 14(13·55) | 5·38 | 0·26 | 39·7% | 33·86 |
| Stowmarket, Suffolk | 15(15·16) | 5·34 | 0·25 | 35·2% | 27·99 |
| Letchworth, Herts. | 15(15·43) | 6·45 | 0·54 | 41·8% | 26·2 |
| Slough, Bucks. | 19(18·88) | 6·58 | 0·51 | 34·8% | 24·2 |
| Sark | 19(19·23) | 5·95 | 0·23 | 30·9% | 35·93 |
| Radlett, Herts. | 19(19·2) | 4·99 | 0·34 | 25·4% | 29·1 |
| Guernsey | 22(21·63) | 5·61 | 0·19 | 25·9% | 40·3 |

| | Differences of means | Standard error of difference |
|---|---|---|
| Melton–Blakeney | 0·87 | 0·35 |
| Radlett–Slough | 0·32 | 0·61 |
| Radlett–Letchworth | 3·77 | 0·63 |
| Letchworth–Melton | 1·88 | 0·59 |
| Guernsey–Sark | 2·4 | 0·29 |
| Sark–Radlett | 0·03 | 0·45 |

the mean for all the localities amounts to about 50 per cent. Comparison of the means with the rainfall for the year shows that though no very close relation obtains, yet there is an obvious tendency for the higher seed contents to be associated with the higher rainfall.

These data indicate that whilst the variation in seed number per fruit is not marked like that of the number of fruits per plant, yet, in respect to both, comparison between species is only valid for comparable environmental conditions. Indeed, the reproductive capacity of a species in a particular environment may well be an important factor in determining its presence or absence. We may add that examination of other species only tends to confirm the conclusions to which the study of the Scarlet Pimpernel, *Anagallis arvensis*, has led us.

The investigation of the distribution of micronutrients in diverse soils is as yet in its infancy, but sufficient evidence is now available to show that these may affect fertility to a greater degree than vegetative growth and could thus play an important role in influencing the abundance and geographical distribution of species. This would appear to be true even of some of the micronutrients that are generally regarded as of less importance. For instance, C. S. Piper has recently furnished experimental evidence to show that Oats can develop normal panicles under conditions of Molybdenum deficiency but fail to produce grains (Piper, 1940). Since the response to micronutrients has been found to differ very appreciably between species and species it may well be that some of the apparent idiosyncracies in geographical distribution of plants are attributable to soil distinctions of this character.

Minute quantities of copper are reported to be necessary to enable both Barley and Flax to set seed, whilst the disease of the fruit of the apple, known as brown core, can be cured by addition of Boron to the soil. The necessity of Boron for fruit production in the Tomato was established by Johnston and Fisher (1929). The growth and yield of both Tomatoes and Rice were found to be stimulated by Vanadium in experiments carried out by Shibuya and Hideski (1934), whilst Scharrer and Schroppe claimed increased yields for Barley, Maize, Oats, Peas, Rye, and Wheat, when supplied with Wolfram. A very considerable number of the trace elements would appear to be necessary for the best growth, the response varying with the species, and from the foregoing it is evident that the outcome of any deficiency may be to reduce or even inhibit reproduction by seed and to diminish any capacity for vegetative spread and multiplication.

The influence of the length of the daylight period upon the reproductive capacity of flowering plants is in general to restrict the area of distribution of the species. The so-called " long-day " species, which require a daily illumination *in excess* of some critical day-length in order to induce flowering, are mostly species of medium or high latitudes liable to flower late or even to remain vegetative towards their southern limits and tending to flower in their natural latitudes following stimulation by the longer days of late spring and summer. Kjellerman as far back as 1878–9 carried out experiments which showed that the arctic Scurvy-grass, *Cochlearia fenestrata*, and the arctic grass, *Catabrosa algida*, flowered later and less freely when the length of

daylight was artificially reduced to twelve hours. The " short-day " species, mostly originating in lower latitudes, tend to flower at their northern limits during the shorter days of spring or autumn, particularly the latter, and so not infrequently their capacity for seed production is there interfered with by the incidence of early frosts. Nevertheless such species may have a more extended northern range if they possess a vegetative means of propagation which is stimulated by the longer period of daily illumination that retards or inhibits reproduction by seed.

It is significant that among the species of wide geographical range, that appear indifferent to photoperiodic stimulation and which flower and fruit alike in regions where and in seasons when the days are either short or long, are ubiquitous weeds such as the Chickweed (*Stellaria media*) and the annual grass *Poa annua*. But since different varieties of the same species may behave differently in this respect, the photoperiodic response is probably not only a factor influencing the geographical distribution of a species and its segregates but may also be a potent influence affecting their survival value. In a few species the response to day length has been shown to be inherited as a simple Mendelian character.

As an example of a long-day species we may cite the woodland Orpine (*Sedum telephium*), which has been shown to have an optimum day length of eighteen hours; diminished daily periods of illumination cause delay in flowering, and if subjected to daily illumination of less than twelve hours the plant will remain vegetative for years. Daniel (1919) found that shading of Lettuces to an extent which did not inhibit flowering or fruiting could nevertheless reduce the fruit production per plant to 5,525 as compared with 78,928 produced by an unshaded plant grown under conditions otherwise similar.

The little weed *Galinsoga parviflora*, a native of tropical South America, which has received the delightful corruption of its latin name " Gallant Soldiers," has become established as a garden weed in Surrey and other parts of south-east England. Despite its provenance this plant will flower in day lengths ranging from nine to twenty-four hours. Not only is it so little influenced by the length of daylight but it will flower with a light intensity of only 8 per cent that of normal daylight, but it does not fruit under these conditions (Shirley, 1929). So, too, the Rosebay Willowherb (*Epilobium angustifolium*) in dull light may form flower buds only to shed them again, illustrating the fact that in general a higher light intensity is requisite for fruit formation than for flower production.

# VI

# THE INFLUENCE OF COMPETITION ON REPRODUCTION

The effect of competition on seed production can be well exemplified by reference to *Ranunculus bulbosus*, of which specimens were examined from a closed meadow community growing on sandy loam and from areas within this community which were maintained in a bare and semi-bare condition, except for the Buttercup plants themselves.

In one respect the three sets of specimens were not comparable, namely that the plants upon the bare ground were not more than two years old whereas some of those in the closed community were probably older. The mode of growth of *R. bulbosus* renders any such difference much less significant than it would be for many species and, if allowance could be made for any such difference of age, it would tend to accentuate rather than to diminish the differences observed. In the semi-closed area there were present, in addition to the plants of *R. bulbosus*, an open community of *Trifolium minus*, *T. repens*, *Veronica arvensis*, *Poa annua*, and *Agrostis alba*. The three sets thus presented three degrees of competition but in other respects were substantially similar.

Actually, owing to the limitations of space and the necessity for avoiding competition between the Buttercup plants themselves, the numbers of plants grown on the bare ground and those subject to slight competition were few. Seventeen plants were grown without competition. The number of fruiting heads which these produced ranged from 4 to 93, with an average of 21·8 fruiting heads per plant. The total number of fertile carpels produced per plant ranged from 113 to 2,939, with an average of 687 carpels. The standard deviation was 615, with a standard error of 149. The number of fertile carpels per fruiting head varied from ten to fifty-six, with a mean value of thirty-two.

Seven plants only were grown subject to partial competition, and these bore from 115 to 530 fertile carpels per plant, with an average of 302 (S.E.M. 116) and a standard deviation of 123·2. The average number of fertile carpels per fruiting head ranged from 5 to 41, with an average of twenty-six.

Of the plants subject to severe competition in the meadow community 118 were examined. These bore from 6 to 234 fertile carpels, with an average of 69 carpels per plant and a standard error of 4·9 (standard deviation 53·29). About 30 per cent of the plants bore under 35 fertile carpels. If we compare the means for the plants on bare soil with those in the meadow the difference is 618 carpels per plant, and the standard error of this difference is 149. That is to say, the difference is more than four times its standard error, and therefore definitely significant. The means for No Competition, Slight Competition, and Severe Competition are 687, 302, and 69 fertile carpels per plant respectively. Although the difference between the mean for the plants subject to slight competition and those not subject to competition on the one hand

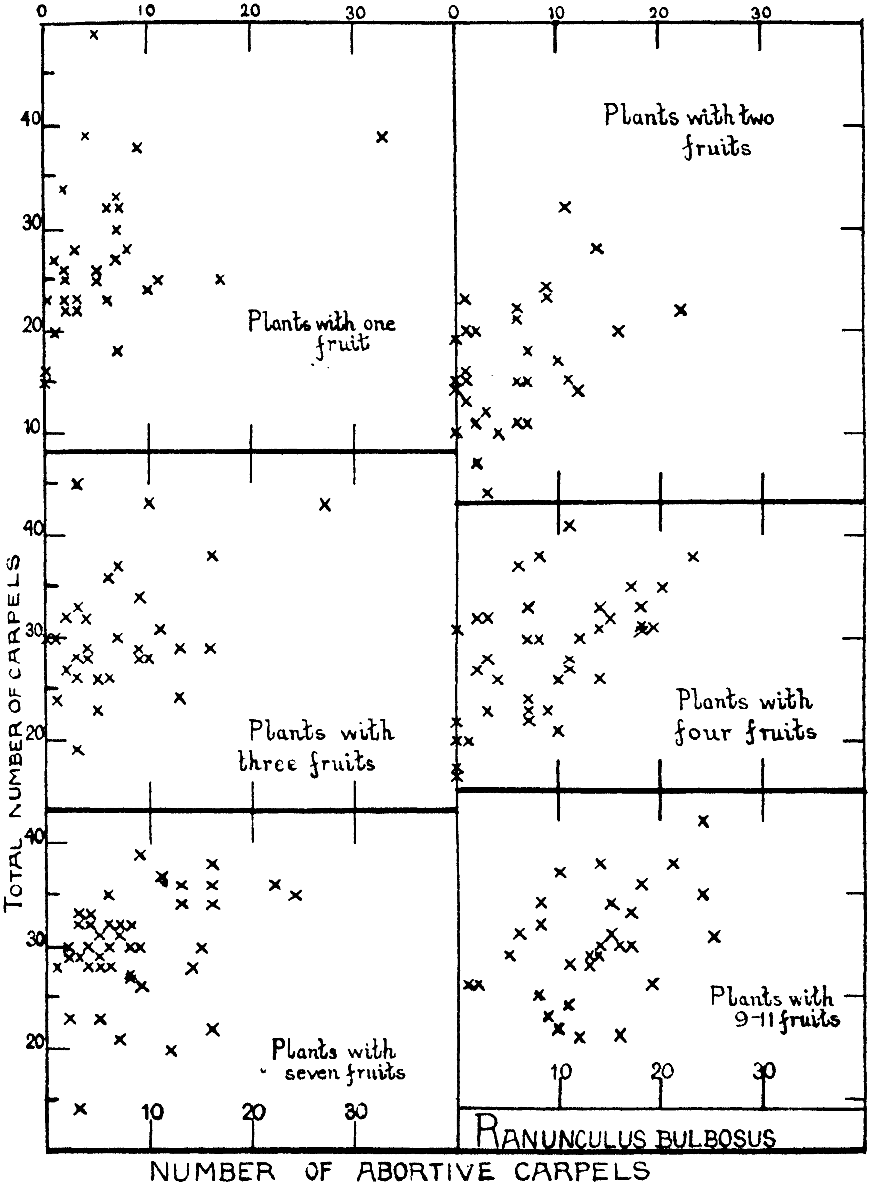



FIG. 8. Diagram showing the relation between the number of abortive carpels and the total number of carpels in plants, bearing different numbers of fruits, of the Buttercup, *Ranunculus bulbosus*. Note that the two tend to increase together, showing the competitive influence.

and subject to severe competition on the other is not "significant," the fact that this mean is intermediate is perhaps noteworthy.

Since the fruits are here achenes containing but a single ovule from the outset there is no complication due to variation in number of seeds per fruit or to competition for food between developing ovules. This was the chief reason why this species was selected for study, since this facilitated comparison between the total number of abortive carpels and the total number produced. This comparison was made for all plants having but a single fruit, and respectively for those having two, three, four, and seven, and those having from 9 to 11 fruits per plant. The number of fruits in the first three categories and the last was 30 and in the other two 40 and forty-two.

In all categories, as shown in the accompanying graphs (Fig. 8), there is a positive correlation between the number of abortive carpels and the total number of carpels, which is slightly more marked as the number of fruits on the plant increases. We have here then fairly clear evidence of internal competition for food, but nevertheless the average number of fertile carpels

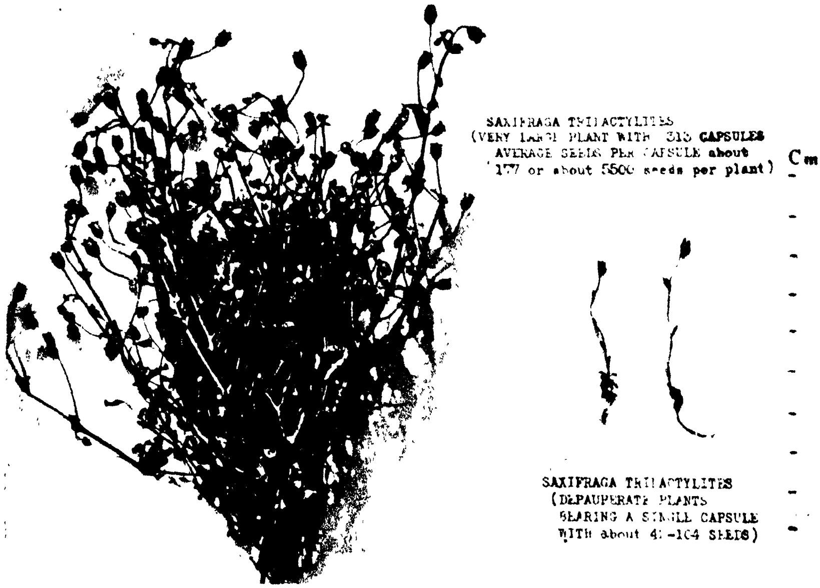
TABLE XX. TOTAL CARPELS AND FERTILE CARPELS OF THE BUTTERCUP, *RANUNCULUS BULBOSUS*

| | Average number of fertile carpels per fruiting head | Average total number of carpels per fruiting head |
|---|---|---|
| Plants with 1 fruiting head | 21·6 | 27·5 |
| ,, ,, 2 fruits | 20·7 | 27·0 |
| ,, ,, 3 fruits | 23·5 | 30·5 |
| ,, ,, 4 fruits | 19·4 | 28·1 |
| ,, ,, 5 fruits | 21·7 | 28·9 |
| ,, ,, 6 fruits | 21·2 | 27·0 |
| ,, ,, 7 fruits | 21·5 | 29·7 |
| ,, ,, 9 to 11 fruits | 21·9 | 35·0 |

remains remarkably constant whether the number of fruits per plant be one, five, seven, nine, or more. All these plants were from the meadow, and since there is here this comparative constancy in number of fertile carpels per fruit (which for all the heads examined has a mean value of 21) the increased number of fertile carpels per fruit in the absence of competition (30) or when this is slight (26) shows that the number of these is determined by nutritional factors rather than by accidents of pollination or fertilization.

We have thus seen that for a species which occurs normally as a constituent of a closed community the removal of the competition factor may increase the reproductive capacity nearly ten times. It is thus evident that we must distinguish between the reproductive capacity of a species in the conditions of competition which obtain in the habitat that the species normally frequents and the potential reproductive capacity in the absence of competition. The former is usually of most biological importance, but the latter may have a bearing on the frequency and abundance of the species in more open types of community. It might perhaps be thought that species which normally occur in open habitats would not show any marked increase of seed production when grown free from competition; but the fact that such species are restricted

PLATE I




Depauperate plants of *Saxifraga tridactylites* bearing a single capsule and producing 42 and 104 seeds and an exceptionally large plant with 313 capsules and producing about 5,500 seeds.

Three flowering plants of *Orobanche elatior* parasitic upon *Centaurea scabiosa*. Each flower will produce about 2,100 seeds.

to situations where competition is slight suggests that they are especially sensitive to its effects.

*Saxifraga tridactylites* is an excellent example of such a species confined to open communities, namely sand dunes, sandy heaths, and the tops of old walls. The fruit production of 160 plants from the two latter habitats is shown in the accompanying Table XXI.

TABLE XXI. FRUIT PRODUCTION IN THE WALL SAXIFRAGE, *SAXIFRAGA TRIDACTYLITES*

| Number of capsules per plant | Number of specimens | Number of capsules per plant | Number of specimens | Number of capsules per plant | Number of specimens |
|---|---|---|---|---|---|
| 1 | 7 | 11 | 3 | 21 | 1 |
| 2 | 27 | 12 | 4 | 22 | – |
| 3 | 19 | 13 | 5 | 23 | 3 |
| 4 | 14 | 14 | 1 | 24 | 1 |
| 5 | 16 | 15 | 2 | 25 | 1 |
| 6 | 8 | 16 | 2 | | |
| 7 | 11 | 17 | 3 | 31 | 1 |
| 8 | 10 | 18 | 2 | 38 | 1 |
| 9 | 6 | 19 | 3 | 46 | 1 |
| 10 | 6 | 20 | 1 | 47 | 1 |

Total 160 plants. Standard deviation 7·69. Average 8 fruits per plant (7·72); S.E.M. 0·60.

The mean number of fruits per plant of *S. tridactylites* is thus eight. The seeds were counted in fifty capsules and were found to range in number from 42 to 287 per capsule, with an average of 143 seeds $\pm 5{\cdot}3$ (143·2) ($\sigma$ 56; S.E.M. 8). The actual numbers were as follows: 42, 44, 52, 63, 63, 76, 84, 97, 98, 98, 102, 104, 106, 108, 109, 113, 118, 121, 122, 123, 124, 131, 131, 131, 133, 135, 145, 146, 153, 156, 156, 162, 169, 169, 171, 171, 179, 180, 189, 205, 210, 213, 218, 220, 221, 233, 238, 239, 287.

The average seed output is therefore $1{,}106 \pm 98$ seeds per plant. Germination tests were carried out which showed an average germination of 70 per cent. Kinzel, who carried out experiments on this species, found that germination only took place in light, and recorded 69 per cent germination. The average reproductive capacity may therefore be assumed to be about 770; probably rather higher, as some of the 30 per cent which fail to germinate in the first year probably do so later. The maximum reproductive capacity for these plants growing under natural conditions would appear to be of the order of 5,000 offspring.

In contrast to this a single plant growing in sandy soil entirely free from competition bore no less than 313 capsules (*cf.* Plate I), with about 143 seeds per capsule, so that the reproductive capacity of this plant was probably somewhere about 32,000, or rather more than six times that of the largest plants found on the walls and heaths. The other extreme is represented by a sample of 43 plants of this species which were obtained from the comparatively dense growth of winter annuals on the medium-aged dunes at Talun-Bach, N. Wales. Of these 23 had but a single capsule, 11 bore two capsules, 6 bore three capsules and there were 3 plants with four capsules. The seeds per capsule numbered about ninety-eight. The average seed

production was therefore only about one hundred and seventy. It can probably be regarded as quite accidental that the effect of eliminating competition has produced so similar an augmentation of reproductive capacity in both *Ranunculus bulbosus* and *Saxifraga tridactylites*. The precise effect of competition may be expected to vary both with the species involved and the climatic-edaphic complex of the environment. We are here only concerned with emphasizing that competition as a factor affecting the reproductive capacity appears to be no less important, sometimes perhaps more so, than climatic or edaphic conditions and hence the importance of reproduction data from plants growing under natural conditions.

In this connection we may emphasize a further aspect of the influence of competition, namely in causing delay in maturity. Some striking examples have been investigated by K. Linkola (1936), who found that in the competition of a meadow community *Trollius europaeus* might not fruit till the eighth year, although in the absence of competition it can fruit in the first season. Similar delay was observed for *Alchemilla vulgaris* and *Geum rivale*, whilst a less pronounced delay was exhibited by *Potentilla erecta*, *Chrysanthemum leucanthemum*, *Ranunculus auricomus*, and *R. acer*. Though all these species are polycarpic, and continue to fruit for a number of years after they attain maturity, so that the loss of 3 to 7 years' output of seeds may be but a small percentage of the total production throughout life, yet the prolongation of the juvenile phase greatly increases the risk of mortality prior to reproduction, and may well be an important factor in determining the capacity of a species to survive in a particular community. A rather extreme example, perhaps, is furnished by *Gentiana lutea*, which, in the absence of competition, will flower in ten years, but in the face of competition may not reach maturity till the lapse of from 20 to 30 years.

Amongst monocarpic species which mostly occur in open communities competition is often pronounced between individuals of the same species. Such plants of waste ground as *Capsella bursa-pastoris* and *Cardamine hirsuta*, of burnt areas on heaths, as *Senecio sylvaticus*, or of clearings in woodlands, such as *Dipsacus pilosus* and *Verbascum thapsus*, to mention but a few examples, exhibit two modes of occurrence. Sometimes they are found as few scattered individuals, often then attaining a large size, or as crowded communities in which small individuals preponderate numerically. Under either condition competition may be chiefly between these individuals rather than with other species. We have already seen that the seeds of depauperate plants, which are frequent in the crowded condition, are usually as viable as those from the larger plants. Where only the one species is involved there is experimental evidence to support the view that the seed crop of the numerous crowded individuals is much the same as that produced by the fewer and larger occupying an equivalent area, so that apart from possible effects of delay in maturation competition between individuals of the same species alone has probably little effect upon reproduction. This is largely an outcome of the fact of which we have furnished experimental proof that the extremely depauperate plants usually produce seed in an amount proportional to their size but quite viable.

# VII

## THE RELATION BETWEEN SEED NUMBER PER CAPSULE AND NUMBER OF CAPSULES PER PLANT

• It is obviously a question of considerable importance with respect to the number of observations requisite for any close approximation to the average seed output, whether the number of seeds in a capsule tends to vary with

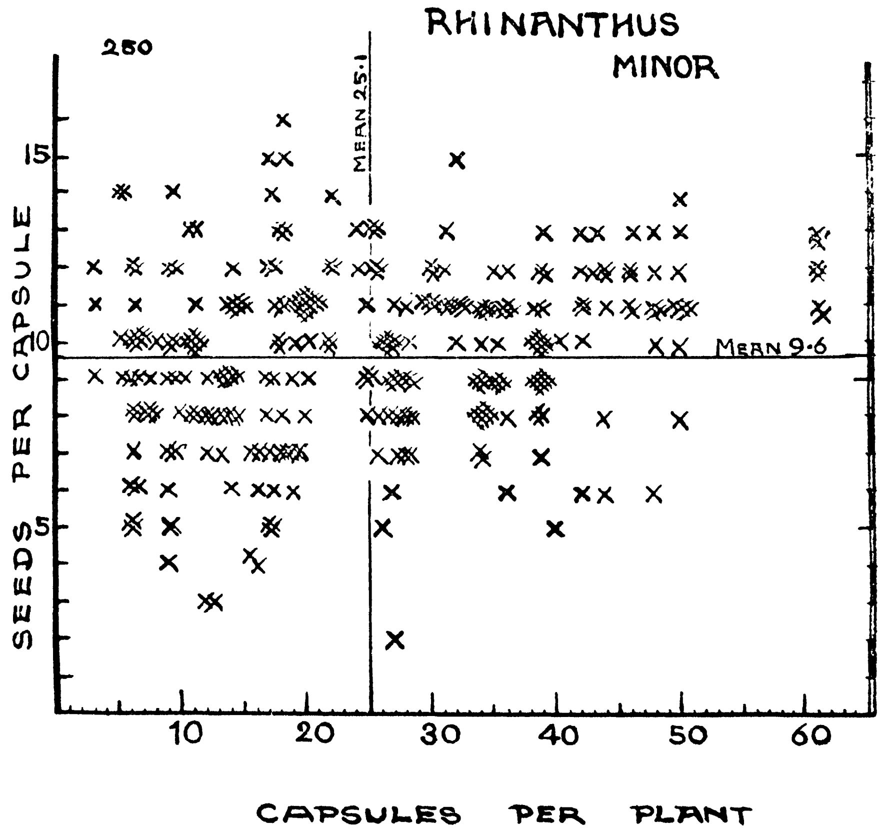



FIG. 9. Diagram showing the absence of correlation between the number of fruits on plants of the Yellow Rattle (*Rhinanthus minor*) Ehrh. and the number of the seeds that the individual fruits contain. The data represent seed counts from 250 capsules from plants bearing from three to sixty fruits.

the number of fruits. If there is any marked degree of correlation between the number of seeds and the number of capsules it is evident that a much greater number of counts of seeds per capsule will be necessary than if there is little or no such correlation. It may be pointed out that in considering this question we can for the present ignore the condition where the individuals are so starved

and depauperate that not only is capsule production reduced to one or two but the lack of nutrition leads to abortion of seeds. Such a state may obtain where habitat conditions are particularly unfavourable, either through severe competition or owing to physical factors; but, apart from a few individuals, such extremes are not usually a feature of the normal habitat of a species, since obviously if they represented any appreciable proportion the species would not survive. Neither have we included the abnormally large specimens grown free from competition on cultivated and manured soil. For our immediate purpose we have utilized specimens taken from natural habitats and including the largest and smallest individuals present. As compared with " random samples " they consequently contain a higher proportion of both extremely small and very large individuals.

The first example we may cite is *Rhinanthus minor* Ehrh. Two hundred and fifty capsules of this species from meadows were examined and the number of seeds were counted in several from each individual plant. In the accompanying correlation diagram (Fig. 9) the numbers of capsules per plant are plotted as abscissae and the average number of seeds per capsule as ordinates.

It is quite obvious that there is no significant correlation between seed number and capsule number in this species, and, indeed, if we compare the largest individuals with 61 capsules with the smallest bearing only three we find that the averages are respectively 12 and 11 seeds. As, however, in this species the number of seeds per capsule is small, *Silene quinquevulnera* was also investigated from this point of view. Here the average number of seeds per capsule is normally about fifty. Capsules were obtained from plants bearing respectively one, three, four, eight, twenty-four, thirty-two, forty-one, and sixty capsules. It will be seen from the accompanying diagram (Fig. 10) that here there is a correlation between seed number per capsule and number of capsules per plant in the depauperate categories with from one to four capsules per individual, but that there is little correlation exhibited in those plants with from eight to sixty capsules.

This would appear to be confirmed by observations on *Silene anglica*, obtained from sandy ground near Tenby, for which the data are given below:

TABLE XXII. SEED NUMBER AND CAPSULE NUMBER IN *SILENE ANGLICA*

| Number of capsules per plant | Average number of seeds per capsule | Number of capsules per plant | Average number of seeds per capsule |
|---|---|---|---|
| 3 | 37 | 13 | 58 |
| 5 | 52 | 14 | 48 |
| 6 | 50 | 17 | 59 |
| 7 | 48 | 24 | 57 |
| 8 | 47 | 96 | 53 |
| 12 | 45 | 103 | 50 |

Both *Silene quinquevulnera* and *S. anglica* thus appear to show that under very impoverished conditions both capsule number and the number of seeds per capsule may be low and that slightly improved conditions are accompanied

by an augmentation in each, but that further improvement, though it gives an increased yield of fruits, has little effect upon the seed contents.

In view, however, of the importance of this relation it was decided to examine a species in which the average number of seeds per capsule was large, hence probably subject to greater range of variation, and in which the capsule number under natural conditions was also very variable. *Glaucium luteum*

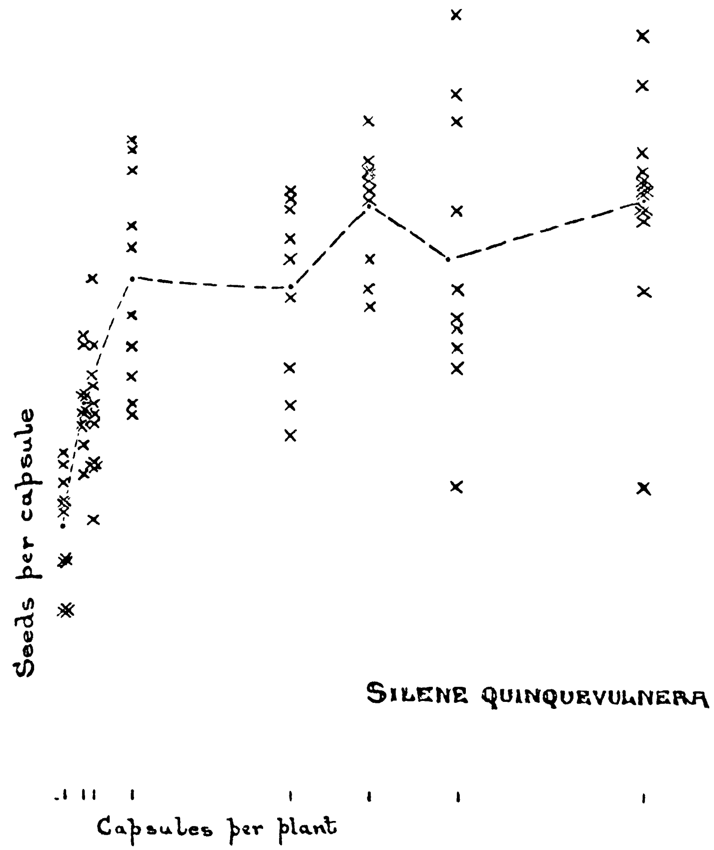



FIG. 10. Relation between the number of seeds per capsule and the number of fruits per plant of *Silene quinquevulnera*. On the depauperate plants bearing only one to five capsules the number of contained seeds increases with the number of fruits. The plants bearing from five to sixty capsules show no significant correlation between these two features.

not only fulfilled these conditions, but material could be obtained, from the shingle beach at Blakeney Point, which grew under conditions that only varied with respect to the accidental circumstances of nutrition. For this purpose 442 capsules were examined and the seed contents carefully counted. They were derived from thirty-five individual plants, and the magnitude of the task can be gauged from the fact that the total number of seeds counted was over one hundred and twenty-four thousand. It is therefore a pleasure to record my indebtedness to members of the Botanical Department of University

College for help received. The number of seeds per pod ranged from 4 to 482, the average seed content being 282±3 seeds (standard error 4·5; standard

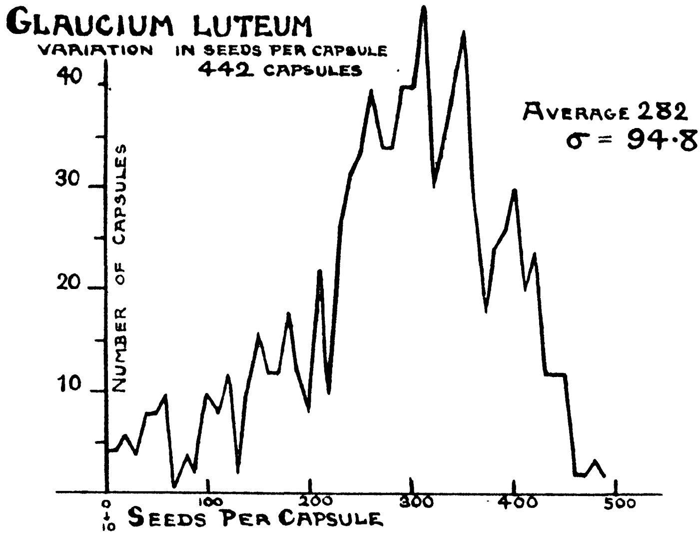



FIG. 11. Diagram showing the variation in number of seeds in 442 capsules of the Sea Poppy (*Glaucium luteum*).

deviation 94·8). The number of pods ranged from six to one hundred and twenty. From the accompanying graph (Fig. 11) it will be realized that

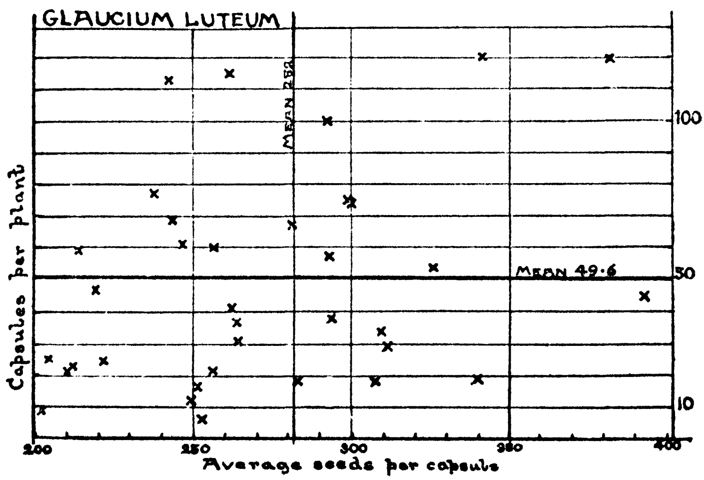



FIG. 12. Diagram showing the absence of any significant correlation between the number of seeds in a capsule and the number of fruits on the plant, for the Sea Poppy (*Glaucium luteum*).

despite the great range in number of seeds there is a reasonable approximation to a normal variation curve. In Fig. 12 the number of capsules per plant is plotted as an ordinate, and the abscissae represent the average number of seeds per capsule. Actually the coefficient of correlation is not only very low

but negative in sign, viz. —0·15, and since the standard error is 0·0465 little significance can be attached to it. It may be added that similar conclusions have resulted from the examination of other species, as, for example, *Anagallis arvensis*, of which forty-two individuals, with capsule numbers ranging from 6 to 237, showed a correlation coefficient of —0·031, with a standard error of 0·15.

We have already cited examples of depauperate plants of *Dianthus prolifer* and *Saxifraga tridactylites* which bore capsules containing a low average number of seeds in comparison with very vigorous individuals of the same species. But the evidence furnished is sufficient to show that a random sampling of capsules from all but exceptionally small or extremely large individuals enables a sufficiently accurate estimate of the average seed content to be obtained. Also, the absence of any significant correlation and the negative values obtained in the examples cited suggest that any tendency towards increase of seed number per capsule that might be induced by more favourable conditions of growth is counterbalanced, or perhaps surpassed, by the competition for food between the developing fruits upon the same individual. Furthermore, there is evidence here for the comparative stability of the reproductive unit.

Another feature of great importance in respect to estimations of seed output will be apparent if we give the additional data to complete our picture of this aspect of *Glaucium luteum*. Of a total of 160 plants examined the range in number of pods per plant is shown in Table XXIII.

TABLE XXIII. FRUIT PRODUCTION IN THE SEA POPPY, *GLAUCIUM LUTEUM*

| Pods per plant | Number of individuals | Pods per plant | Number of individuals | Pods per plant | Number of individuals | Pods per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 14 | 12 | 7 | 23 | 3 | 57 | 1 |
| 2 | 13 | 13 | 4 | 26 | 1 | 60 | 1 |
| 3 | 11 | 14 | 3 | 32 | 2 | 65 | 1 |
| 4 | 18 | 15 | — | 35 | 2 | 67 | 1 |
| 5 | 9 | 16 | 1 | 37 | 1 | 69 | 1 |
| 6 | 10 | 17 | 2 | 39 | 1 | 76 | 1 |
| 7 | 8 | 18 | 3 | 42 | 1 | 100 | 1 |
| 8 | 10 | 19 | 2 | 43 | 2 | 112 | 1 |
| 9 | 7 | 20 | 2 | 46 | 1 | 115 | 1 |
| 10 | 3 | 21 | — | 48 | 1 | 120 | 2 |
| 11 | 4 | 22 | 1 | 55 | 1 | 218 | 1 |

The range is seen to be from 1 to 218, with a mean pod production of 17, the standard deviation being 12·6 and the standard error of the mean 1·83. The mean seed output is therefore approximately 4,800 seeds ±398, whilst the maximum seed production was probably of the order of 61,000 seeds, or about thirteen times that of an average plant. It will be at once apparent, as one might expect from the operation of the factor of competition, that whilst there are numerous individuals with few capsules there are a relatively small number with many. Thus, whilst the mean number is 17 the modal number

is four. Hence it is that the modal seed output is probably only about one-quarter of the average seed output. If seed production be estimated by determining the seed production of " an average individual," as, for example, in the determinations for weeds made by Stevens (1932), it is the modal value that is more likely to be approximated to. But it is the average rather than the modal value which is likely to have the greatest biological significance. The average output weight is 4·6 gm.

The type of occurrence with a high proportion of small individuals has already been exemplified by the two annual species *Cardamine hirsuta* and *Saxifraga tridactylites*, and is particularly marked in monocarpic species of poor soils, where careful examination of the habitat usually reveals that the

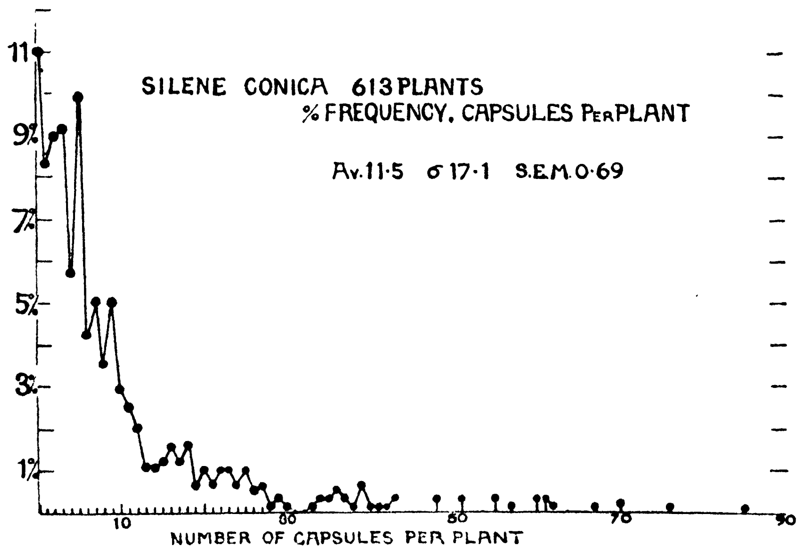



FIG. 13. Diagram showing the percentage frequency distribution for the number of capsules on 613 plants of *Silene conica*. Note that the largest proportion of individuals bear but a single capsule and about 70 per cent bear less than the average number of capsules per individual based on the entire population.

larger and therefore more conspicuous individuals are numerically inferior. This is particularly well shown by data obtained over a number of seasons for 613 plants of *Silene conica* (*cf.* Table XXX) in which the range in number of capsules per plant was from 1 to 284, with a mean value of 11·5 capsules (S.E.M. 0·69) and a standard deviation of 17·1. The average number of seeds per capsule was 68 (range 24–98). The mean seed output is therefore 784 seeds per plant. The average germination is 98 per cent, so that the average reproductive capacity for the species is 768 per plant. The accompanying graph (Fig. 13) shows, however, that the mode is a plant with but a single capsule, and actually about 70 per cent of the individuals produce less than the average number of capsules.

It is true of most monocarpic species that have prolonged fruiting periods that after the initiation of reproduction the number of fruits in process of

development increases as the fruiting period proceeds. This is particularly marked in members of the Caryophyllaceae, where, owing to the dichasial character of the inflorescence, the number of fruits maturing at successive stages of the plant's growth tends towards a geometrical progression with a common ratio of two. It is, however, frequently true only of the earlier phases of development that the number of fruits at any one stage is double that of the preceding age class, due to abortion or retardation of some of the ultimate potential ramifications of the infructescence. But it is clear that despite the compensatory effects of the addition of assimilatory organs there is an increasing demand on the food supply, so that, if we compare the seed contents of capsules at successive stages, we can test upon the same plant the reality of the competition between fruits which we have already hypothesized.

For this purpose we have utilized *Lychnis Githago*. The various age classes have been determined by (*a*) their position; and (*b*) the colour changes of the testas. The use of this second criterion is desirable owing to the occasional retardation of fruit development, as compared with the age indicated by position of capsules on the lateral branches.

Four age classes of capsules could be segregated by both position and colour, and the data for these are furnished in Table XXIV. From this it will be seen that the capsules of successive age classes show a slight initial rise in the number of contained seeds, followed by a steady decrease. This latter clearly demonstrates the reality of the internal competition factor.

TABLE XXIV. SEED NUMBERS IN CAPSULES OF SUCCESSIVE AGE CLASSES OF THE CORN COCKLE, *LYCHNIS GITHAGO*

| Age class | Minimum | Maximum | Mean | S.E.M. | Standard deviation |
|---|---|---|---|---|---|
| 1st formed capsules | 10 | 36 | 30·7 | 1·4 | 5·8 |
| 2nd Age class | 20 | 39 | 32·6 | 0·85 | 3·7 |
| 3rd Age class | 20 | 36 | 28·9 | 0·67 | 3·59 |
| 4th Age class | 7 | 27 | 17·3 | 0·67 | 5·08 |

It will be realized that the capsules of depauperate plants correspond to those of the first (if they bear but one capsule) or earlier age classes of the capsules borne on larger plants which are either immune from, or only suffer slightly by, the prior claims of fruits already maturing. The slight initial rise is not perhaps surprising, since though the first formed capsule is doubtless the most favourably situated as regards products of assimilation the supply of nutrients from the soil probably materially augments with the growth of the root system, and the availability of these might well be the limiting factor in preventing the first capsules from producing as many seeds as those of the next age class. It is the augmentation of both root system and the assimilatory surface that is partly responsible for the fact that diminution of seed number is not proportional to the increase in fruit number; but there is also the stability of the reproductive unit, to which reference has already been made, which is expressed in the tendency towards complete abortion of a considerable proportion of the potential flower rudiments on the ultimate ramifications with a measure of proportionality between fruit number and food supply, so that

we find fewer more or less normal sized capsules rather than the full potential complement of appreciably smaller capsules. It is as if, within rather wide limits of variation, there were some kind of quantum law obtaining with respect to this organic unit as well as to the individual seeds it contains.

These considerations show us that though there may be appreciable variation between capsules upon a large plant the average production of seeds per capsule as between different individuals varies far less than might have been expected.

# VIII

# THE COMPARATIVE STUDY OF SEED OUTPUT AND REPRODUCTIVE CAPACITY

## GEOGRAPHICAL RANGE AND SEED OUTPUT

With a view to obtaining an insight into the possible factors that have influenced the evolution of the diverse reproduction rates exhibited by different species a comparative study has been made of the seed output and reproductive capacity of various types.

*Scilla species*

The first examples that we purpose to consider are the British species of *Scilla*. These are three in number, and are all Oceanic types, differing markedly, however, in their range. As regards their European distribution the Wild Hyacinth (*Scilla nutans*) is the most widespread, extending northwards to Holland and eastwards as far as Germany, but becoming increasingly more common westwards. The Spring Squill (*Scilla verna*), though its range northwards extends to Norway and southwards to Spain, has a much more limited distribution and is practically confined to the Atlantic seaboard, whilst the Autumn Squill (*Scilla autumnalis*) is rather more southern and still more restricted in its range. The distribution in Britain shows the same decrease of range,[1] as is well illustrated if we compare the comital frequencies. The comital frequency is the number of counties or vice-counties from which the species has been recorded as a wild plant, expressed as a percentage of the total number of such divisions, and was devised by the writer as a convenient means of numerical expression of frequency (*cf.* E. J. Salisbury, " The East Anglian Flora " (1932)). These frequencies are as follows:

| | COMITAL AND VICE-COMITAL FREQUENCY [2] (PER CENT) | | | |
|---|---|---|---|---|
| SPECIES | *England* | *Scotland* | *Ireland* | *Mean for Britain* |
| Scilla nutans | 98·6 | 92·7 | 100 | 97·1 |
| Scilla verna | 18·3 | 39·0 | 17·5 | 24·7 |
| Scilla autumnalis | 14 | 0 | 0 | 4·7 |

We can reasonably infer from these facts that the three species have a decreasing toleration for a wide range of climatic conditions, or, put in other terms, *Scilla nutans* has the least specialized demands on the habitat conditions and *Scilla autumnalis* the most. It may be added that cultivation of these species shows that under the same climatic conditions *S. autumnalis* is the least easily grown in the heavier types of soil, *S. nutans* will tolerate a very

[1] These figures are taken from Matthews, J. R. (1937), " Geographical Relationships of the British Flora," *Journal of Ecology*, XXV, 1–90.

[2] For distribution maps of *S. verna* and *S. autumnalis*, *cf.* E. J. Salisbury (1939), "Ecological Aspects of Meteorology," *Quart. Jour. Roy. Met. Soc.*, LXV, 337–58.

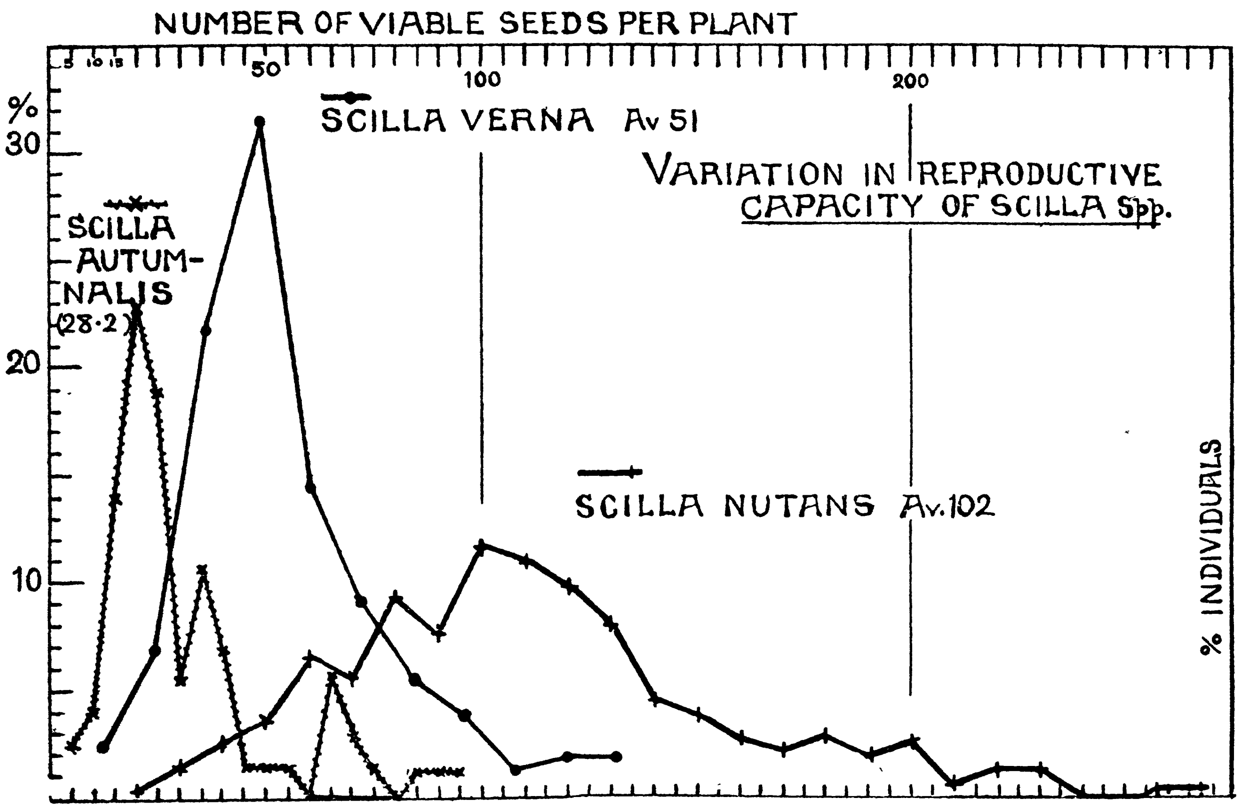



FIG. 14. Variation in reproductive capacity of three species of *Scilla*, based on the percentage frequency distribution of the number of seeds per plant and the average proportion of viable seeds. Note that the mode and mean is lowest for the rarest species and highest for the common Wild Hyacinth (*Scilla nutans*). The Spring Squill (*S. verna*) is intermediate both in frequency and reproductive capacity.

wide range of edaphic conditions, whilst *S. verna* is more or less intermediate in its particularity. It can then be also inferred that the risks of mortality will be greatest for *S. autumnalis* and least for *S. nutans;* therefore, on the orthodox view, we should expect that the seed output would be greatest for *Scilla autumnalis*, least for *S. nutans*, and intermediate for *Scilla verna*. These three species were therefore studied as to their seed output and germination, and tests were made of seeds from wild plants so that their "reproductive capacities" could be determined. The number of plants investigated were: 76 of *Scilla autumnalis;* 166 of *Scilla verna;* and 484 of *Scilla nutans*. The average germination for *S. nutans* and *S. verna* was practically the same, viz. 94 per cent, but for *S. autumnalis* was appreciably lower, viz. 83 per cent. In the accompanying graph (Fig. 14) the reproductive capacity, as estimated on the basis of the number of capsules produced by the different individuals and the average number of seeds per capsule, is presented as a frequency curve. It is at once obvious that the order of the reproductive capacities of the three species is the very reverse of that which we should expect if the orthodox view were valid. It may be urged, of course, that the larger seed production of *S. nutans* as well as the heavier character of its seeds is necessitated by the fact that it grows in a more advanced type of plant community than the two other species, but these latter both grow in habitats of similar competitive status. Our study of these three species suggests, then, that seed production is not conditioned mainly by the potential mortality but is perhaps one of the factors which make for the success of a species, and that *S. nutans* is the commonest of the three, partly owing to its larger seed production and heavier seeds, and that the two other species which have seeds of similar weight and occupy similar habitats have frequencies that bear some relation to their reproductive capacities.

## THE SUNDEWS (*Drosera* species)

The next genus we shall consider from this standpoint is *Drosera*. Of the Sundews there are three British species, all of them rosette plants with small seeds, and occupying almost identical types of habitat. The variation in seed character within the genus is marked. Of these three species, two, namely *Drosera rotundifolia* and *Drosera anglica*, possess very similar seeds, those of the latter being slightly larger. They are both fusiform, very light (*ca.* 0·000022 gm.), flattened, and small. The seeds of *Drosera intermedia* are so entirely different in character as to warrant placing it in a different section; they are rounded and more compact. There can be little doubt that the seeds of *D. intermedia* are less easily dispersed than those of its congeners. Another feature to which attention may be called is the high proportion of seeds in the capsules of *D. intermedia*, which, even from visual examination, are manifestly abortive.

The comital and vice-comital frequencies (percentages) are as follows:

| | England | Ireland | Scotland | Mean for Britain |
|---|---|---|---|---|
| Drosera anglica | 47·8 | 87·5 | 80·5 | 71·9 |
| Drosera intermedia | 62·0 | 47·5 | 31·7 | 47·0 |
| Drosera rotundifolia | 98·6 | 100·0 | 97·6 | 98·7 |

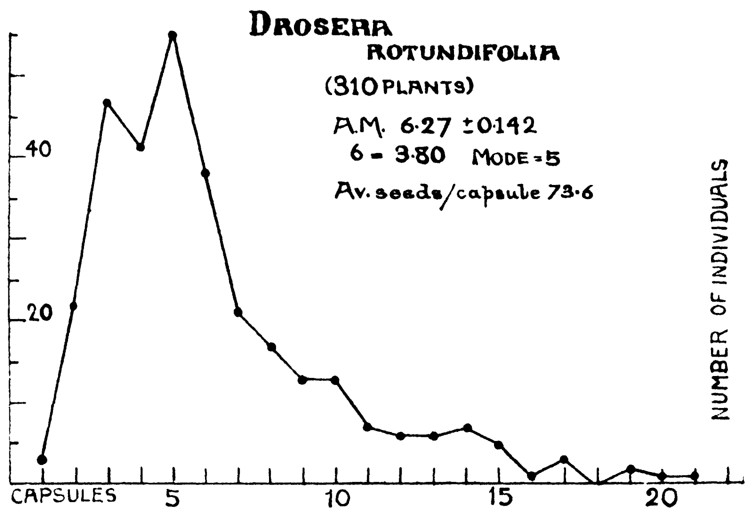



FIG. 15. Frequency distribution for the number of capsules per plant of the Common Sundew (*Drosera rotundifolia*). Data for 310 individual plants. Ordinates represent number of individuals, abscissae the number of capsules.

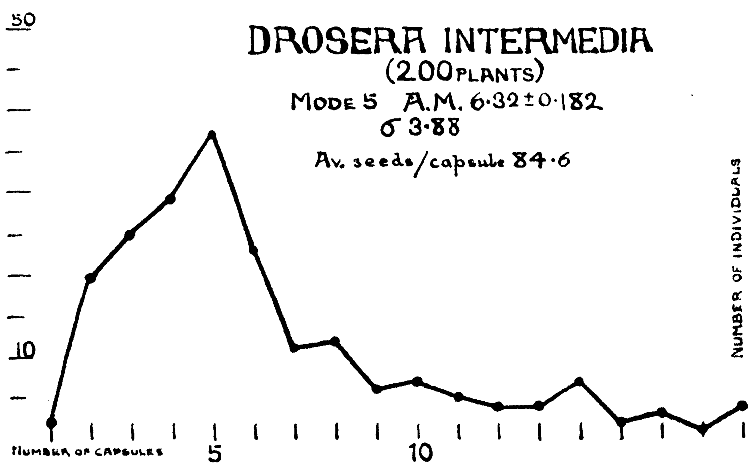



FIG. 16. Frequency distribution for the number of capsules on 200 plants of *Drosera intermedia*.

It is then evident that *D. rotundifolia* is easily the most frequent as it is also the most abundant. *D. anglica* follows, although less frequent in England, and *D. intermedia* is the least frequent. In England, where *D. anglica* is often rather local, *D. intermedia* is more frequent, but though in such areas as the Dorset heaths the latter is the more abundant species it is generally true that *D. anglica* is more abundant than *D. intermedia.*

The variation in capsule number for the three species is illustrated in the accompanying graphs (Figs. 15, 16, and 17). It will be seen that the modes are the same for all three species (viz. 5 capsules per plant) and the averages

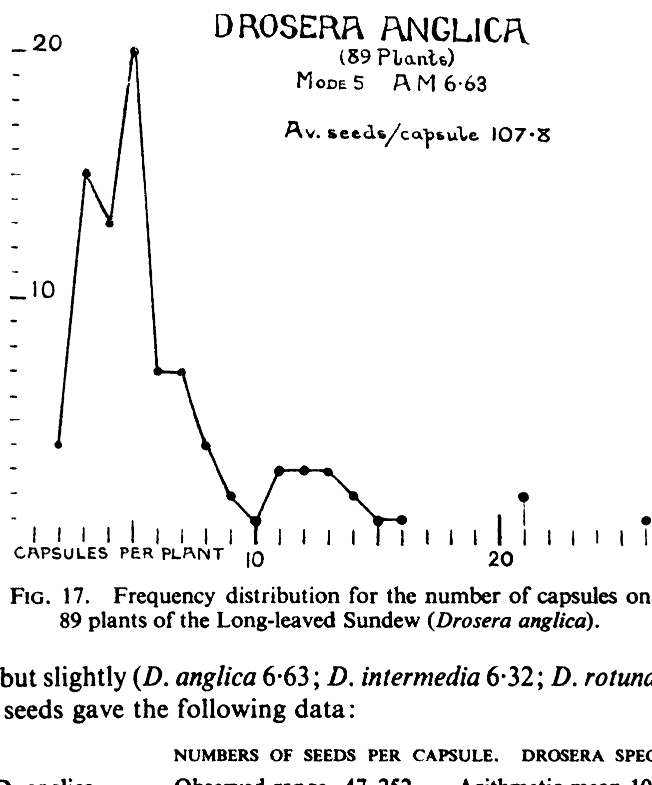



FIG. 17. Frequency distribution for the number of capsules on 89 plants of the Long-leaved Sundew (*Drosera anglica*).

also differ but slightly (*D. anglica* 6·63; *D. intermedia* 6·32; *D. rotundifolia* 6·27). Counts of seeds gave the following data:

NUMBERS OF SEEDS PER CAPSULE. DROSERA SPECIES

| | | | | |
|---|---|---|---|---|
| D. anglica | Observed range | 47–252 | Arithmetic mean | 107·8 |
| D. intermedia | ,, ,, | 51–111 | ,, ,, | 84·6 |
| D. rotundifolia | ,, ,, | 52–113 | ,, ,, | 73·6 |

It should be emphasized that the above figures for *D. intermedia* omit the obviously non-viable seeds. The average output of seeds on the basis of these data is therefore: *D. anglica*, 716 seeds per plant; *D. rotundifolia*, 462 seeds per plant; and *D. intermedia* 535 seeds per plant. There is here nothing to suggest that the orthodox view may not be correct, except that one would expect a larger seed production from *D. intermedia* than from *D. anglica*. Germination tests have been carried out successfully, employing many hundreds of seeds of both *D. anglica* and *D. rotundifolia*. I have been unable to germinate *D. intermedia*, but Kinzel furnishes data for all three species. For *D. anglica* the percentage germinations ranged from 14 to 24 per cent,

whilst Kinzel obtained 10 per cent with this species, and we shall not be far wrong in assuming that the average germination is about 16 per cent. For *D. rotundifolia* my own tests averaged 28 per cent, whilst Kinzel obtained 31 per cent. For *D. intermedia* Kinzel gives the germination as only 2 per cent. In the accompanying graph (Fig. 18) the reproductive capacities, estimated on the basis of these germination data, are presented for the plants examined. The vegetative method of reproduction which the writer described for *D. intermedia* and *D. rotundifolia* from laboratory material (Salisbury, E. J. (1915), " On the occurrence of Vegetative Propagation in *Drosera* ") does

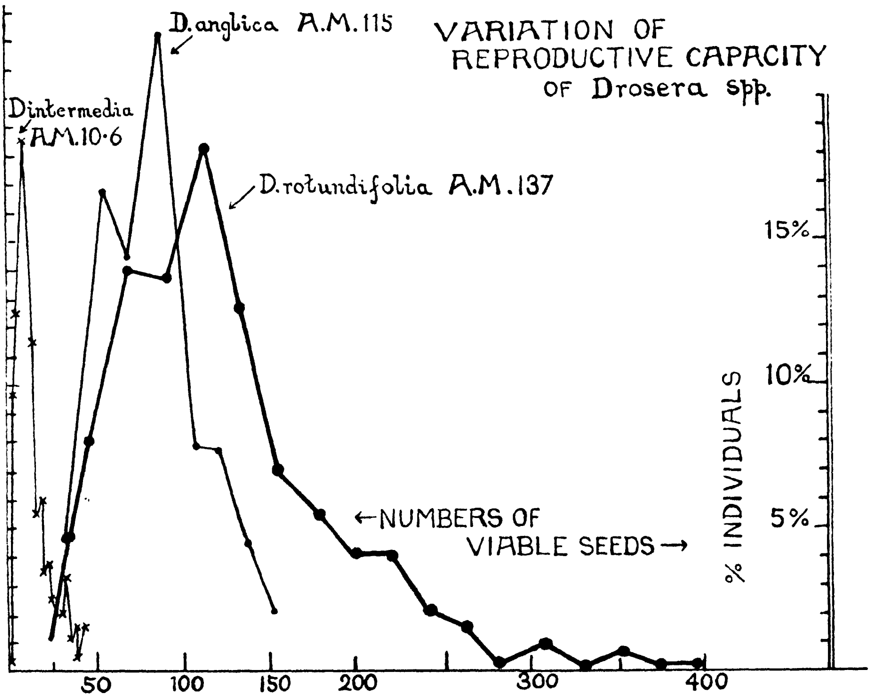



FIG. 18. Variation in reproductive capacity of the three British species of Sundew (*Drosera*). Note the much higher reproductive capacity of the common species, *D. rotundifolia*, and the low reproductive capacity of the very local *D. intermedia*.

also occur in nature, but is not of sufficient frequency materially to affect the reproductive capacity of the species. It will be at once obvious that the sequence of reproductive capacities exhibits precisely the same relationship to relative frequency of the species concerned as was obtained for the genus *Scilla*. Here again, then, the evidence would appear to controvert the orthodox interpretation and to support the view that increase of reproductive capacity is one of the factors tending to promote increased frequency. It may be emphasized that, even if the average germination of *D. intermedia* were as much as ten times that observed by Kinzel, the same sequence would still hold.

The very considerable numbers of all three kinds of Sundew which are sometimes to be seen on wet areas of heaths after burning of the taller vegeta-

tion suggests that mortality is mainly conditioned by competition with other plants rather than by animal or fungal parasites or predators, which renders it the more probable that the relative frequencies and abundance of these species of *Drosera* is inversely correlated with the risks of mortality.

Attention may also be drawn to the fact that the extremely light, orchid-like seeds of *D. rotundifolia* and *D. anglica* (Fig. 1) are very readily dispersed by the wind but that those of *D. intermedia*, being more compact and the inflorescence stalks being appreciably shorter, the seeds are much less readily dispersed. So that on these grounds alone we should have anticipated a larger seed production for this species if the magnitude of the seed output be mainly conditioned by the risks attendant upon survival. Actually from these data the average reproductive capacity of *D. intermedia* is 10·7.

TABLE XXV. (A). VARIATION IN NUMBER OF CAPSULES PER PLANT IN SPECIES OF *DROSERA*

| Number of capsules per plant | Number of individuals of *D. anglica* | Per cent | Number of individuals of *D. rotundifolia* | Per cent | Number of individuals of *D. intermedia* | Per cent |
|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 3 | 1 | 2 | 1 |
| 2 | 4 | 4·4 | 22 | 7·7 | 19 | 9·5 |
| 3 | 15 | 16·6 | 48 | 16·0 | 25 | 12·5 |
| 4 | 13 | 14·4 | 41 | 13·6 | 29 | 14·5 |
| **5** | **20** | **22·2** | **55** | **18·3** | **37** | **18·5** |
| 6 | 7 | 7·7 | 38 | 12·7 | 23 | 11·5 |
| 7 | 7 | 7·7 | 21 | 7·0 | 11 | 5·5 |
| 8 | 4 | 4·4 | 17 | 5·7 | 12 | 6·0 |
| 9 | 2 | 2·2 | 13 | 4·3 | 6 | 3·0 |
| 10 | 1 | 1·1 | 13 | 4·3 | 7 | 3·5 |
| 11 | 3 | 3·3 | 7 | 2·3 | 5 | 2·5 |
| 12 | 3 | 3·3 | 6 | 2·0 | 4 | 2·0 |
| 13 | 3 | 3·3 | 6 | 2·0 | 4 | 2·0 |
| 14 | 2 | 2·2 | 7 | 2·3 | 7 | 3·5 |
| 15 | 1 | 1·1 | 5 | 1·7 | 2 | 1·0 |
| 16 | 1 | 1·1 | 1 | 0·3 | 3 | 1·5 |
| 17 | | | 3 | 1·0 | 1 | 0·5 |
| 18 | | | | | 4 | 2·0 |
| 21 | 2 | 2·2 | | | | |
| 26 | 1 | 1·1 | | | | |
| Totals | 89 plants | | 310 | | 201 | |
| Averages | 6·63 capsules | | 6·27 capsules | | 6·32 capsules | |
| S.E.M. | 0·44 | | 0·21 | | 0·277 | |
| $\sigma$ | 4·2 | | 3·80 | | 3·88 | |

(B). VARIATION IN NUMBER OF SEEDS PER CAPSULE *DROSERA* SPECIES

D. anglica Huds. 47, 54 (2), 71, 72, 74, 84 (2), 95 (3), 105, 106, 108, 109, 112, 113, 115, 118, 121, 126, 127, 128, 131, 139 (2), 145, 252.
Average 108 (107·8)±4·8. $\sigma$ 38·29. S.E.M. 7·2.

D. rotundifolia L. 52, 56, 57, 58, 60, 63, 65, 66 (3), 67, 71, 76, 77, 78, 81, 82, 92, 98, 102, 113.
Average 74 (73·6)±3. $\sigma$ 15·9. S.E.M. 4·5.

D. intermedia Hayne (D. longifolia L.). 51, 55, 64, 76, 92 (2), 93, 102, 110, 111.
Average 85 (84·6)±4·4. $\sigma$ 20·8. S.E.M. 6·7.

## THE POPPIES (PAPAVER species)

So far we have considered two genera, the species belonging to which occupy very different habitats but are constituents of relatively advanced communities. We shall now consider a third genus, viz. *Papaver*, all the species of which, both here and on the continent, are plants of open habitats and most usually encountered as cornfield weeds. From the data already furnished in Table I, it will be seen that the seed weights of all the four British species are very similar, ranging from an average of 0·000128 gm. for *Papaver dubium* to 0·000158 gm. for *Papaver hybridum*. In all, the seeds are contained in a capsule which opens by pores immediately beneath the stigmatic disk, borne on a stalk that is stiff at maturity. Thus for all four species the dispersal mechanism is the same, depending upon the jerking out of the seeds through these pores when the stiff stalk alternately bends and recoils under the influence of gusts of wind. The distance to which the seeds are carried when they are shot out of the pores similarly depends upon wind action but also upon the height above ground-level at which the pore is situated. The average height of the capsule is significantly different for each of the four species, so that, having regard to their similarity in other respects, they afford an opportunity of comparing the magnitude of the seed production with the efficiency of dispersal, and experiments with this aim will be described later (*cf.* Fig. 19).

The geographical range of the four species also shows marked differences. *Papaver Rhoeas* is very similar in this respect to *P. dubium;* but though both are almost equally widespread in England and Ireland, *P. dubium* is less so in Scotland, and there can be no question that in general it is much less abundant than *P. Rhoeas.* The other two species are both southern-continental types, of which *P. hybridum* is much less widespread in Ireland and absent from Scotland. *P. hybridum* is undoubtedly the more rare, but despite the rather wide distribution of *Papaver Argemone* it only persists over any period of years in restricted areas. Its particularity may be instanced by its occurrence over an area of less than half an acre in part of an arable field on sandy loam near Radlett. Here it has persisted, to the writer's own knowledge, for a number of years, despite the considerable diversity of cropping, but except for slight seasonal fluctuations the area over which the species occurred has remained substantially the same. We have, then, two common species and two uncommon species, with an appreciable distinction in respect to both frequency and abundance between the two members of each pair, giving us an order of increasing rarity, in both senses, namely *P. Rhoeas*, *P. dubium*, *P. Argemone*, and *P. hybridum.*

Of the two common species, data were obtained readily, and an appreciable number of specimens were examined from each locality and in each season. But for the two uncommon species the numbers of specimens from individual localities were often few and the data have of necessity been obtained from a considerably larger number of stations over a period of years.

The variation in capsule number per plant is shown in Table XXVI, from which it will be seen that all four species illustrate the feature, to which attention has already been drawn, namely the high proportion of small

TABLE XXVI. VARIATION IN NUMBER OF CAPSULES PER PLANT IN SPECIES OF *PAPAVER*

| Capsules per plant | P. Argemone | P. dubium | P. hybridum | P. Rhoeas |
|---|---|---|---|---|
| 1 | 29 | 101 | 36 | 34 |
| 2 | 31 | 106 | 54 | 23 |
| 3 | 40 | 79 | 50 | 51 |
| 4 | 19 | 39 | 26 | 42 |
| 5 | 16 | 29 | 16 | 29 |
| 6 | 9 | 27 | 12 | 25 |
| 7 | 7 | 16 | 16 | 17 |
| 8 | 13 | 19 | 5 | 17 |
| 9 | 19 | 18 | 7 | 18 |
| 10 | 1 | 11 | 9 | 16 |
| 11 | 5 | 5 | 6 | 11 |
| 12 | 6 | 9 | 4 | 9 |
| 13 | 7 | 8 | 7 | 7 |
| 14 | 1 | 7 | 1 | 6 |
| 15 | 4 | 9 | 4 | 4 |
| 16 | 3 | 9 | 4 | 6 |
| 17 | 0 | 2 | 3 | 8 |
| 18 | 2 | 5 | 1 | 4 |
| 19 | 0 | 0 | 1 | 7 |
| 20 | 1 | 2 | 0 | 8 |
| 21 | 1 | 4 | 0 | 6 |
| 22 | 1 | 0 | 0 | 5 |
| 23 | 1 | 3 | 3 | 3 |
| 24 | 1 | 0 | 2 | 3 |
| 25 | 0 | 2 | 0 | 2 |
| 26 | 0 | 2 | 0 | 5 |
| 27 | 1 | 0 | 0 | 4 |
| 28 | 1 | 0 | 1 | 2 |
| 29 | 0 | 0 | 1 | 0 |
| 30 | 1 | 2 | 0 | 2 |
| 31 | 1 | 0 | 0 | 1 |
| 32 | 0 | 2 | 1 | 2 |
| 33 | 0 | 0 | 0 | 2 |
| 34 | 1 | 0 | 0 | 0 |
| 35 | 1 | 1 | 0 | 0 |
| 36 | 0 | 0 | 0 | 1 |
| 37 | 2 | 0 | 1 | 1 |
| 38 | 0 | 2 | 0 | 0 |
| 40 | 0 | 0 | 1 | 1 |
| 42 | 0 | 0 | 0 | 2 |
| 43 | 0 | 0 | 2 | 0 |
| 45 | 0 | 0 | 0 | 1 |
| 46 | 0 | 0 | 0 | 1 |
| 47 | 1 | 0 | 1 | 1 |
| 48 | 0 | 0 | 0 | 1 |
| 49 | 0 | 0 | 0 | 1 |
| 50 | 0 | 1 | 1 | 1 |
| 51 | 0 | 2 | 0 | 1 |
| 55 | 0 | 0 | 0 | 2 |
| 57 | 0 | 1 | 0 | 0 |
| 61 | 0 | 0 | 1 | 1 |
| 62 | 0 | 0 | 1 | 0 |
| 69 | 0 | 0 | 1 | 0 |

TABLE XXVI. VARIATION IN NUMBER OF CAPSULES PER PLANT IN SPECIES OF *PAPAVER*—*continued*

| Capsules per plant | P. Argemone | P. dubium | P. hybridum | P Rhoeas |
|---|---|---|---|---|
| 70 | 0 | 0 | 0 | 1 |
| 71 | 1 | 1 | 0 | 0 |
| 72 | 0 | 0 | 0 | 1 |
| 75 | 0 | 1 | 1 | 0 |
| | | Also 94, 100, 104, and 116 capsules | | Also 87, 118, 120, 232, and 342 capsules |
| Total number of plants | 227 | 529 | 277 | 401 |
| Total capsules | 1,548 | 3,616 | 2,019 | 5,021 |
| Average capsules per plant | 7 (6·81)±0·33 | 7 (6·83)±0·34 | 7 (7·28)±0·42 | 12 (12·5)±0·6 |
| Standard deviation | 7·4 | 11·8 | 10·55 | 18·4 |
| Standard error of mean | 0·50 | 0·51 | 0·63 | 0·92 |

individuals. But though the modes are as follows: 3 capsules for *P. Argemone*, 2 capsules for *P. dubium* and *P. hybridum* and 3 for *P. Rhoeas;* yet the respective means are 6·81, 6·83, 7·28, and 12·5. Thus an assessment of seed production based upon the examination of what would appear to be an " average " specimen in the material examined would have resulted in an estimate that would be less than one-third the actual mean for *P. dubium* whilst for *P. Rhoeas* it would be less than one-quarter. Only on the basis of a careful statistical examination is it safe to judge what the " average " specimen of a species actually is, and selecting a so-called average capsule for seed counting may be just as misleading.

The number of seeds in capsules of *Papaver* is always large and their counting a laborious and time-consuming occupation, so that the numbers of capsules examined are fewer than could have been wished. Without deliberately including very depauperate specimens or abnormally vigorous ones I have examined both small and large capsules from normal plants so as to obtain a better idea of the range involved, hence the deviations and probable errors of the means are perhaps somewhat exaggerated.

Seeds were counted in thirty capsules of *P. Argemone* and totalled nine thousand four hundred and nine. The lowest number of seeds per capsule was 78 and the highest six hundred and seventy-four. The mean number was 313·6±17·7, with a standard deviation of 147·1 and S.E.M. 26·8. Thirty-eight capsules of *P. hybridum* yielded 8,743 seeds, the number per capsule ranging from 26 to six hundred and fifteen. The mean was 230±14·4 ($\sigma$ 135·1; S.E.M. 21·9). Of *P. dubium* twenty-five capsules were examined, and contained from 600 to 4,004 seeds. The mean number of seeds per capsule was 2,008±126, with a standard deviation of 945 and a standard error of one hundred and eighty-nine. The seed contents of one hundred capsules was weighed and the number of seeds estimated. The weighing method gives values which are too high, owing to the inclusion of abortive seeds and capsular fragments; nevertheless the mean value obtained in this way of 2,585 seeds per capsule does suggest that the mean based upon actual counts of the apparently viable seeds is rather on the low side.

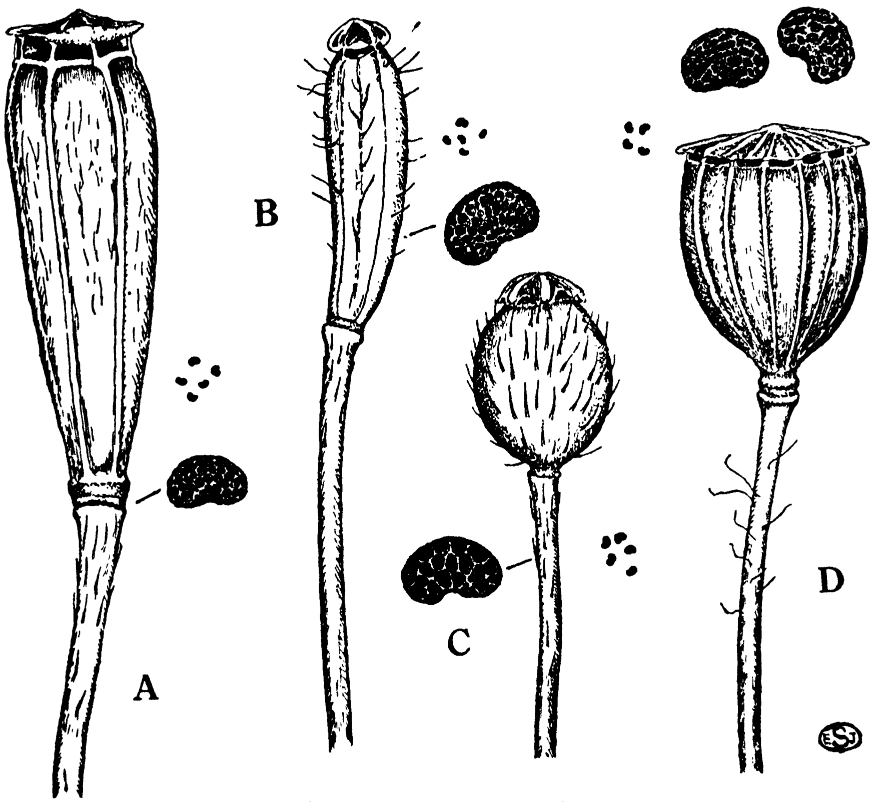



FIG. 19. Capsules and seeds of the four British species of Corn Poppy (*Papaver* species). The seeds are shown on the same scale as the capsules and also on a larger scale to show the sculpturing: (A) *Papaver dubium;* (B) *Papaver Argemone;* (C) *Papaver hybridum;* (D) *Papaver Rhoeas.*

Of *P. Rhoeas* the contents of thirteen capsules only were actually counted, and contained from 463 to 2,556 seeds, with a mean value of $1{,}360 \pm 125$ seeds per capsule and a standard deviation of 678 and S.E.M. of one hundred and eighty-eight. The entire seed contents of sixty other capsules were weighed and gave a mean value of 1,480 seeds per capsule, which is sufficiently close to that obtained by counting to warrant the belief that the latter is approximately correct.

From the foregoing data the average seed output per plant would thus be, for *Papaver Rhoeas* 170,000 seeds, for *P. dubium* 13,700 seeds, for *P. Argemone* 2,142 seeds, and for *P. hybridum* 1,680 seeds.

I am indebted to Miss E. M. Cooper, B.Sc., and Miss M. Lawford, B.Sc., for carrying out a number of germination tests for these four species. The average of these and other tests, as well as such records as the literature affords, yield the following mean values:

| | | |
|---|---|---|
| Papaver Argemone | 63 | per cent germination |
| Papaver dubium | 42 | per cent germination |
| Papaver hybridum | 91 | per cent germination |
| Papaver Rhoeas | 48 | per cent, plus 16 per cent. Delayed total 64 per cent. |

In the accompanying Table XXVII the mean reproduction data are summarized and the average reproductive capacities calculated.

TABLE XXVII. REPRODUCTION DATA FOR BRITISH SPECIES OF *PAPAVER*

| Species | Mean number of capsules per plant | Mean number of seeds per capsule | Mean percentage germination | Mean reproductive capacity |
|---|---|---|---|---|
| Papaver Argemone | 6·81 ± 0·38 | 313·6 ± 17·7 | 63 | 1,347 ± 140 |
| Papaver hybridum | 7·28 ± 0·42 | 230 ± 14·4 | 91 | 1,529 ± 183 |
| Papaver dubium | 6·83 ± 0·34 | 2,008 ± 126 | 42 | 5,757 ± 669 |
| Papaver Rhoeas | 12·5 ± 0·6 | 1,360 ± 125 | 64 | 10,928 ± 1,522 |

If we assume that for *P. dubium* and *P. Rhoeas* the mean values for numbers of seeds per capsule obtained by weighing are more nearly correct than those based on actual counts of the good seeds in a much smaller number of capsules, then the mean reproductive capacities for these two species would be: 7,331 for *P. dubium* and 11,840 for *P. Rhoeas*, changes in magnitude that do not materially affect the relations between the species.

It will be at once evident that the reproductive capacities of the two common species are far greater than of the two uncommon species, and that the sequence of increasing magnitude of reproductive capacity corresponds for three of the species with their increased frequency of occurrence. The results, then, are fully in accord with those obtained for *Scilla* and *Drosera* species, except for *P. hybridum*, which though rarer than *P. argemone* has a slightly higher reproductive capacity. But it is significant that the germination of the seeds of *P. hybridum*, like those of *P. dubium*, is of the type I have designated "simultaneous," whereas the germination of the seeds of *P. Argemone* and *P. Rhoeas* is naturally "intermittent." As I have elsewhere shown (*cf.* E. J. Salisbury (1929), "The Biological Equipment of Species") the delayed germination of a portion of the seed crop is an important insurance against adverse climatic conditions, especially for "Southern" types.

Observations were made on the seedling mortality of the various species of *Papaver*. For this purpose comparison must be made between the two summer annuals *P. Rhoeas* and *P. Argemone* and the two winter annuals *P. dubium* and *P. hybridum*. Of the former the mortality of *P. Argemone* is much the higher. Of the latter, during a moderately severe winter the mortality for *P. dubium* was 57·5 per cent and of *P. hybridum* from 48 to 75·9 per cent. The lower mortalities for the latter species were observed where there was some slight protection from wind frosts not shared by the seedlings of *P. dubium*. It is, then, safe to say that in the winter and spring germinating species alike, the higher mortality rate is found in the species with the lower seed output.

Turning now to the consideration of the dispersal efficiency of these species a considerable number of measurements were made, to the nearest centimetre, of the height of the capsule pores above the ground-level. For *P. dubium* such measurements were made for three hundred capsules during two seasons, one of which was rather wet and the other rather dry.

The mean value from season to season varies by from 8 to 13·7 per cent.

The measurements of the other species were less numerous but were also obtained during more than one season. The mean values are given below:

TABLE XXVIII. HEIGHT OF CAPSULE PORES ABOVE GROUND-LEVEL IN *PAPAVER* SPECIES

| Species | Number measured | Range in centimetres | Mean height of pores in centimetres | $\sigma$ | S.E.M. |
|---|---|---|---|---|---|
| Papaver hybridum | 119 | 16–43 | 26 (25·8) | 5·1 | 0·46 |
| Papaver Argemone | 211 | 14–65 | 35 (35·2) | 10·72 | 0·71 |
| Papaver dubium | 300 | 21–98 | 56 (56·3) | 14·27 | 0·82 |
| Papaver Rhoeas | 151 | 32–88 | 58 (57·6) | 9·5 | 0·77 |

Difference between means for *P. Argemone* and *P. hybridum* 9·4 cm.; standard error of difference 0·846

" " " *P. Rhoeas* and *P. dubium* 1·3 cm.; S.E.D. 1·12.

Experiments were carried out on the seed dispersal of *P. dubium*, *P. Argemone*, and *P. hybridum*. The method adopted was to obtain newly dehisced capsules of the three species with fruit stalks as nearly as possible of the average length. Each in turn was then fixed at its base so that the poral openings were exactly at the average height for the species concerned, and was then placed in front of an electric fan. Between the fan and the capsule was fixed a shutter, by means of which the wind could be cut off at will. In this way the gusts of wind in nature were simulated, whilst at the same time a practically constant wind velocity was assured. On the far side of the capsule a roll of paper, with a matt surface to prevent rolling of the seeds, was spread out in the direction of the wind current and was marked with parallel lines at intervals of 1 cm. at right angles to the main direction of seed travel. The capsules of each species were in turn subjected to the same conditions with respect to the length of each exposure, the number of " gusts," and the duration of the experiment. But the artificial " gusts " were for each a similar sequence of varying durations. After each experiment the seeds in each distance-interval-class were counted. The results for the three species expressed as percentages, are shown in the accompanying graph (Fig. 20). It will be realized that, for all, the " curves " are surprisingly similar, although even these show the greater efficiency for dispersal which the increased height of the capsules of *P. dubium* confer. If, however, we consider the absolute number of viable seeds per plant which attain the longer distances the differences of efficiency are seen to be appreciable, and it is, of course, these absolute differences which are important. Thus, grouping the longer distances, the following data are obtained, utilizing the reproductive capacity data furnished above.

| DISTANCES IN CENTIMETRES | NUMBER OF VIABLE SEEDS WHICH WOULD BE FURNISHED BY ONE PLANT | | |
|---|---|---|---|
| | *P. dubium* | *P. argemone* | *P. hybridum* |
| 176–325 | 155 | 63 | 25 |
| 326–375 | 3·2 | 0 | 0 |
| Over 375 | 1·61 | 0 | 0 |

It is evident, then, that even under these conditions of equivalent wind velocities the efficiency of dispersal varies with the height of the capsule, and

when it is remembered that at these low heights, under natural conditions, the wind velocity itself augments with increase of height above the ground, it will be at once apparent that the order of efficiency of dispersal has almost certainly the same sequence for these four species as the mean heights of their

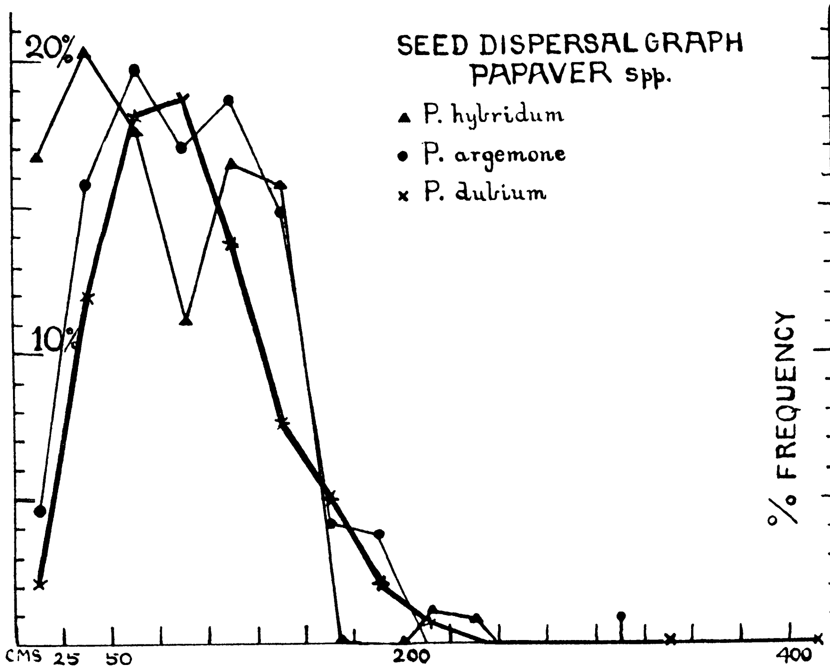



FIG. 20. Diagram representing the percentage distribution of the seeds of three species of *Papaver* when the capsules are placed at their average heights and subjected to the same variations of wind velocity. The distances to which the seeds were carried have been grouped into distance classes differing by 25 cm. Ordinates represent the percentage of the total number of seeds shed by each species which were carried to the particular group of distances. The abscissae represent the grouped distances to which the seeds were carried.

capsules, and this, be it noted, is precisely the sequence of increasing frequency. Here again, on the orthodox view, we should have expected the decreasing efficiencies of dispersal to be compensated for by an increased productivity. Thus we are once more led to the conclusion that reproductive capacity is not merely a life insurance, a purely defensive measure, but a positive asset that surpasses the needs imposed by mortality and provides for the occupancy of fresh territory. Such an interpretation is fundamentally different from that adopted by Herbert Spencer in his " Principles of Biology," where he stated that there was " a major adjustment of average multiplication to average mortality " (1894, Vol. II, p. 401).

# IX

# REPRODUCTION BY SEEDS IN RELATION TO LIFE SPAN

If the development of reproductive capacity be in any appreciable degree connected with the probable mortality amongst the offspring then we should expect that the seed production of annual species would be high as compared with that of perennials. If we imagine a perennial species of which the normal duration of its fruiting phase is twenty years, then, if the amount of seed produced be merely a matter of ensuring the adequate filling of gaps due to mortality, we should expect such a species might produce each year about one-twentieth of a similar but annual species. Indeed, unless the seeds of the annual species exhibited marked dormancy the annual production by the perennial of a twentieth part would be more likely to ensure survival than the much larger harvest in a single season of the annual. It is true, as we have noted for trees with mast seasons, that an exceptional production of seedlings in a particular season may result in survival which does not obtain when the seedlings are few, but such is probably only a feature of species with markedly fluctuating productivity. Wherever predators or parasites attack particular species in a wholesale manner the numbers of these are conditioned by the average frequency of their prey, and hence we cannot assume that an annual species would gain any advantage from the necessity of producing all its offspring in a single season. It is true that the perennial species usually requires one or more seasons to attain maturity, but, as I have elsewhere stressed (Salisbury (1933)) mortality in plants is mainly a feature of the seedling stage, so that it is at least doubtful whether any appreciable augmentation of the seed production would be necessitated by the delay in maturity.

It is unfortunately difficult to obtain pairs of species which are respectively annual and perennial that are comparable in other respects. Clearly a comparison of, for example, *Mercurialis perennis* with its extensive vegetative propagation, and *Mercurialis annua*, or *Ajuga reptans* and *A. chamaepitys*, would be unjustified, and even where no conspicuous vegetative propagation occurs the two species should be of similar habit and dimensions.

*Meconopsis cambrica* affords a perennial species which can reasonably be compared with the annual poppies, being plants of similar bulk and having seeds of similar size, though the perennial, being a woodland type, has, as we should expect from the evidence already afforded, rather heavier seeds, so that the seed production would be lower than if the seeds had the same weight as in *Papaver*.

A total of 102 plants of this species were examined for capsule production and the seed contents were counted in twenty capsules. The data are furnished in Table XXIX.

TABLE XXIX. CAPSULE PRODUCTION OF WELSH POPPY, *MECONOPSIS CAMBRICA*

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 2 | 2 | 11 | 6 | 20 | 3 | 29 | 1 |
| 3 | 4 | 12 | 5 | 21 | 2 | 38 | 1 |
| 4 | 8 | 13 | 2 | 22 | 3 | 39 | 2 |
| 5 | 6 | 14 | 1 | 23 | 2 | 42 | 1 |
| 6 | 10 | 15 | 4 | 24 | 1 | 45 | 1 |
| 7 | 4 | 16 | 3 | 25 | 1 | 46 | 1 |
| 8 | 7 | 17 | 1 | 26 | 1 | 59 | 1 |
| 9 | 6 | 18 | 2 | 27 | 1 | 69 | 1 |
| 10 | 5 | 19 | 1 | 28 | 1 | 80 | 1 |

$\sigma$ Standard deviation 13·6. Total 1,502 capsules on 102 plants.
Average 14·7 capsules per plant.
S.E.M. 1·34.
$\sigma$ Standard deviation 13·6.
Seeds per capsule 305 to 750. Average 497·3 seeds per capsule; S.E.M. 29·9.
$\sigma$ 134. Average seed output 7,310 seeds per plant.

The average seed output of the four species of *Papaver* already considered ranges from 1,680 seeds per plant for *P. hybridum* to 17,000 for *P. Rhoeas*. The mean seed production of *P. Rhoeas* and *P. dubium* both exceed that of *Meconopsis cambrica* in a single season (viz. 7,310) and the same relation holds if we compare the estimated maximum production in one season of the specimens examined, which is approximately 40,000 seeds for *M. cambrica*, 465,000 for *P. Rhoeas*, and 50,000 for *P. dubium*. As, however, the percentage germination of *P. Rhoeas* and *P. dubium* is often rather low whereas that of *M. cambrica* is frequently high, the reproductive capacity of the latter in a single season is perhaps not far inferior to that of the annuals. It is very evident that the perennial has an enormously greater reproductive capacity when the number of years during which it continues to fruit is taken into account. I have elsewhere called attention to the lamentable dearth of data respecting the span of life of perennial species, and the only evidence that can be furnished for the fruiting period of *M. cambrica* is that more than one specimen, " self-sown " in the writer's garden, has been fruiting for 10–11 years without showing any indications of old age. Some of the larger wild specimens from N. Wales which provided the data cited in Table XXIX supplied indications that they may have been much older. It may also be noted that the annual seed output of *M. cambrica* is about one and a half times that of the normally monocarpic *Glaucium luteum*.

## SOLANUM SPECIES

### Black Nightshade, *Solanum nigrum* L.

An interesting comparison is furnished by the Black Nightshade (*Solanum nigrum* L.), an annual of waste places, and the Woody Nightshade (*Solanum Dulcamara* L.), a perennial climber most frequent in scrub and woodland

margins on basic soils. Sixty-eight plants of *S. nigrum*, comprising all the individuals from several separate areas, yielded a total of 16,171 fruits. The smallest individual bore fifteen fruits, whilst the largest bore three thousand six hundred and ten. The average number of berries was $238 \pm 37$ per plant ($\sigma$ 454; S.E.M. 55·3). The number of seeds per berry was counted in a random selection of one hundred fruits as follows: 6 (1), 7 (1), 26 (1), 27 (3), 28 (2), 92 (4), 30 (2), 31 (4), 32 (5), 33 (4), 34 (6), 35 (4), 36 (7), 37 (8), 39 (5), 40 (3), 41 (5), 42 (4), 43 (4), 44 (3), 45 (3), 46 (5), 47 (2), 48 (3), 50 (3), 51 (2), 52 (1). A total of 3,585 seeds, or an average of $35{\cdot}85 \pm 0{\cdot}5$ ($\sigma$ 7·5; S.E.M. 0·75).

On the basis of these data the average seed output is $8{,}039 \pm 844$ seeds per plant. Germination tests yielded an average of 90 per cent, so that the average reproductive capacity is approximately $7{,}800 \pm 819$ potential offspring per plant.

Woody Nightshade, *Solanum Dulcamara* L.

For this species the data obtained were few. Fruit counts were made on eight adult plants and ranged from 346 to 4,416 berries per plant, with a total of 11,167 berries, or an average of $1{,}396 \pm 316$ per plant ($\sigma$ 1,327; S.E.M. 474). The seeds per berry in thirty-six specimens ranged in number from 9 to 63, as follows: 9, 11, 14, 16, 26, 28, 30, 31, 33, 34, 36 (2), 37 (2), 38, 40 (4), 41 (3), 42 (4), 43 (4), 50, 51, 54, 55, 59, 63. The average is $38 \pm 1{\cdot}3$ ($\sigma$ 12·1; S.E.M. 2·0). These data denote an average output of $53{,}459 \pm 13{,}822$ seeds per plant, or somewhere between forty and seventy thousand seeds. Germination appears to range from about 70 to 90 per cent, with an average value of 79 per cent, so that the reproductive capacity would be $42{,}232 \pm 11{,}919$. In view of the small number of specimens on which the fruits were counted no great importance attaches to the precise figures, especially as the eight individuals were probably rather below the average size that adult plants would attain when exempt from all human interference. A plant of *S. Dulcamara* will live for twenty years at least, probably much longer, so that it is probable that the total potential progeny of a well-grown individual would during its lifetime number well over three-quarters of a million. Moreover it is evident that even in a single season the potential offspring are about five times as numerous as those of its annual congener.

The seeds of *S. Dulcamara* are known to be widely distributed by birds, and probably those of *S. nigra* also. As the data cited in this book show, even under favourable conditions of artificial culture the seedlings of *S. nigrum* exhibit an average mortality of 7·5 per cent, and this may be as high as 19 per cent, which suggests that the mortality under natural conditions, even when there is no competition, may be considerable. No exact data for *S. Dulcamara* can be given, but observations suggest that the seedling mortality is probably low in the absence of competition. Thus, the difference in output does not appear to be related to the risks of mortality.

## Silene Species

It may be urged that both the examples already dealt with compared an annual species of open habitats with a perennial species that occupies in the one instance woodland and in the other scrub or wood margin. Thus, the

perennial species might be held to suffer more from competition, which would necessitate a larger reproductive rate. This is, of course, in a measure true, though it is hardly possible to assume that such increased risk is proportional to the increased rate of reproduction. The mortality is much greater in these woodland species largely because of the much higher reproduction rate. However, the species of the genus *Silene* afford a comparison between species that alike occupy open habitats. For this purpose we can compare the annual species *Silene conica* and *Silene anglica* with *Silene dubia*, a perennial species of rocky habitats, and *Silene otites*, a perennial species of sandy heaths. The variation in the number of capsules born on 613 plants of *S. conica* is shown in Table XXX, where, incidentally, it will be observed that there are more individuals bearing a single capsule than are found in any other category of capsule number. Apart from this there is indication of a mode in the region of 6 capsules, but the actual arithmetic mean is 11·5 capsules per plant. The observed range was from 1 to 284 capsules, but although six specimens, or

TABLE XXX. VARIATION IN NUMBER OF CAPSULES IN *SILENE CONICA*

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|
| 1 | 67 (11%) | 21 | 6 (1%) | 41 | 1 (0·1%) |
| 2 | 51 (8·3%) | 22 | 4 (0·6%) | 42 | 1 (0·1%) |
| 3 | 54 (9%) | 23 | 6 (1%) | 43 | 1 (0·1%) |
| 4 | 56 (9·1%) | 24 | 6 (1%) | 48 | 2 (0·3%) |
| 5 | 35 (5·7%) | 25 | 4 (0·6%) | 51 | 2 (0·3%) |
| 6 | 59 (9·9%) | 26 | 6 (1%) | 55 | 2 (0·3%) |
| 7 | 26 (4·2%) | 27 | 3 (0·5%) | 57 | 1 (0·1%) |
| 8 | 30 (5%) | 28 | 4 (0·6%) | 60 | 2 (0·3%) |
| 9 | 21 (3·5%) | 29 | 1 (0·1%) | 61 | 2 (0·3%) |
| 10 | 30 (5%) | 30 | 2 (0·3%) | 62 | 1 (0·1%) |
| 11 | 18 (2·9%) | 31 | 1 (0·1%) | 67 | 1 (0·1%) |
| 12 | 15 (2·5%) | 32 | 0 | 70 | 2 (0·3%) |
| 13 | 13 (2%) | 33 | 0 | 76 | 1 (0·1%) |
| 14 | 6 (1%) | 34 | 3 (0·5%) | 85 | 1 (0·1%) |
| 15 | 6 (1%) | 35 | 2 (0·3%) | 102 | 1 |
| 16 | 8 (1·2%) | 36 | 2 (0·3%) | 124 | 1 |
| 17 | 10 (1·6%) | 37 | 3 (0·5%) | 129 | 1 |
| 18 | 8 (1·2%) | 38 | 2 (0·3%) | 134 | 1 |
| 19 | 10 (1·6%) | 39 | 1 (0·1%) | 147 | 1 |
| 20 | 4 (0·6%) | 40 | 4 (0·6%) | 284 | 1 |

Total 613 plants

Average 11·5±0·46 capsules per plant. $\sigma$ 17·1; S.E.M. 0·69.

about one per cent, of the individuals bore over one hundred capsules 78 per cent bore less than fourteen capsules (*cf.* Fig. 13). The average number of seeds per capsule was 68±3·2, with an observed range of from 24 to 98 (standard deviation 19·3; standard error of mean 4·8). The average of a number of tests for germination was 98 per cent when the season was sunny and dry, although in wet seasons in this country the germinative capacity of the seeds may be low.

The average seed output of *S. conica* is therefore 784±84 seeds per plant and the average reproductive capacity 768 offspring per plant.

It should be stated that these specimens were obtained during a period of years, and that in one season when the numbers of individuals was high their size was small and the average was only five capsules per plant: an outcome not so much of competition with the grasses of the sandy heaths as of the dry season.

The second annual species we shall consider is *S. anglica*, a plant of sandy cornfields. Forty-eight individuals were examined and the range in number of capsules was from 3 to one hundred and three. The average number of capsules was 17 (16·9)±1·9, with a standard deviation of 20·2 and a standard error of the mean of 2·9. Seed counts were made in seventy undehisced capsules and showed a range from 25 to 68 seeds per capsule, with a mean value of 48±0·7 seeds ($\sigma$ 9·34; S.E.M. 1·11). The average germination in this species is about 80 per cent, so that the average reproductive capacity is about 573 offspring per plant; a reproductive capacity, be it noted, less than half that of the two rarer species of *Papaver*. Yet, having grown all these species and observed their seedling mortality, one can assert that the mortality risk for *S. anglica* is greater and not less than that for even the rarest British species of *Papaver*.

Turning our attention now to two perennial species of this genus, *S. otites* is found in semi-open communities on the Breckland heaths, sometimes growing in company with *S. conica*. Seventeen plants showed a range in capsule number from 27 to 263, with an average of 94±11 capsules per plant ($\sigma$ 68·4; S.E.M. 16·6).

One hundred capsules of this species were found to contain from six to thirty-nine seeds each, with an average seed content of 23 (23·2±0·46). The standard deviation was 7·1 and the standard error of the mean 0·7. Thus, the average seed output was 2,186±299 seeds per plant. The average germination observed was 65 per cent, so that the average reproductive capacity is 1,421 offspring per plant per annum.

Of the rare *S. dubia* only ten plants were available. These yielded from 30 to 338 capsules, with an average of 122·4±5·2 capsules per plant ($\sigma$ 107·4; S.E.M. 7·8). The seeds per capsule ranged from 48 to 120, with an average of 84·1±5·2 ($\sigma$ 24·2; S.E.M. 7·8). The average seed output of this species is thus about 10,300 seeds.

So, whereas the two annual species of open habitats have seed outputs of 782 seeds and 811 per plant, those of the two perennial species of open habitats are respectively 2,187 and 10,300 seeds per plant per annum; and when we consider the reproductive capacities the relation remains much the same. Neither of these perennial species of *Silene* have a long life span, but if we take a conservative estimate of eight or nine years only, their potential progeny outnumber those of the annual species by from 16 to 100 times.

One other comparison may be cited, namely the perennial *Scrophularia nodosa* and the biennial *Scrophularia vernalis*, both woodland species, though the former endures the lower light intensity. Sixty-one plants of *S. nodosa* L. were examined for fruit production, and the number of fruits ranged from

42 to 956 per plant. The total number of capsules counted was 14,354, or an average of 235±16 capsules per plant ($\sigma$ 187; S.E.M. 24).

Sixteen capsules were examined for seed content, and the number of seeds ranged from 105 to two hundred and seventy-two. The sixteen capsules contained 3,266 seeds, or an average of 204±8·6 seeds per capsule ($\sigma$ 51·68; S.E.M. 12·92). Thus, the mean seed output from these data would be 48,077 ±5,225 seeds per plant per annum, or, in round numbers, between 43,000 and 54,000 seeds. Germination in the light is about 60 per cent, so that the mean reproductive capacity would be about 27,884±3,030 potential offspring each year. The seeds, which are dispersed by wind, are small in size, of light weight and pitted (*cf.* Fig. 1).

It is of interest to note that Eklund gives data for six capsules of this species which yield a much lower average, namely 105 seeds per capsule. He also gives the numbers of fruits per plant for two individuals, viz. 60 and seventy-six. These data would, if typical, suggest a much lower productivity in Scandinavia than with us.

*S. vernalis* L. will sometimes bear many more flowers than *S. nodosa*, and one specimen examined produced no fewer than 3,969 capsules. Commonly, however, the number of capsules is much fewer and the average is probably not more than about one thousand two hundred. The seeds per capsule average about 38, so that the average seed output would be under 45,600, or probably not significantly different from the annual product of *S. nodosa*.

# X

# THE SEED PRODUCTION OF PARASITES, SAPROPHYTES AND SEMI-PARASITES

The seed output of Parasites and Saprophytes has for long been assumed to be high, since it is clear that, if random dispersal of the seeds by wind be the method of distribution, there must inevitably be a very high proportion of wastage from seeds coming to rest where no suitable host is available or where there is no adequate organic nidus. It is manifest, too, that amongst the parasites such wastage will be the greater the more specialized the parasite as regards its restriction to few species of host plants, or, in extreme instances, to a single species of host. Further, the wastage will be greater as the hosts or host are of increasing rarity.

## THE GENUS OROBANCHE (BROOMRAPES)

The genus *Orobanche* provides unique material for testing whether there are adequate grounds for the assumption that the seed production is more or less proportional to the normal wastage. It is evident that no parasitic species could survive if the seed production were so low as not to admit of such wastage as normally obtains, so that a specialized parasite with a low seed output could not survive unless the density of its host plant was such that an appreciable proportion of the seeds could not fail to reach appropriate hosts. But the generally accepted view involves more than this, and implies that the seed production is proportional to the normal wastage. There appears, however, to be no adequate data for such an assumption, which has been based on *a priori* reasoning rather than on ascertained facts. An illustration of the fact that all parasites do not produce very large numbers of seeds is furnished by *Dactylanthus Taylori* Hook. f., a monotypic representative of the Balanophoraceae, endemic to New Zealand. It attacks a variety of host plants, but, according to L. B. Moore (1940), the average seed output is only between 1,500 and 2,000 seeds per plant. In the genus *Orobanche* we fortunately have species which are relatively unspecialized, like *Orobanche minor*, capable of attacking a diversity of hosts, and also specialized species such as *Orobanche hederae*, confined to a single species of host, but that a widespread one, or *Orobanche elatior*, which is restricted to *Centaurea Scabiosa*, a much more localized host than the Ivy, whilst *Orobanche picridis* would appear to occupy a more or less intermediate position with respect to its biological specialization since it occurs on *Picris*, *Dipsacus*, and some Umbelliferae, although probably attacking a smaller range than *O. minor*.

### *Orobanche minor* Sm.

This species not only attacks a wide range of hosts, but some of these, such as *Trifolium repens*, are both widespread and abundant.

The number of capsules per plant varies considerably, according to the

vigour of the host, from as few as four to as many as ninety (*cf.* Table XXXI (A)). One hundred and twenty-five plants yielded an average of 23·8±0·74 capsules per plant ($\sigma$ 13·2; S.E.M. 1·1). According to Wentz the average number of seeds per capsule is one thousand five hundred. Accepting this figure, the seed production may be taken as averaging some 35,000 seeds per plant.

TABLE XXXI (A). VARIATION IN CAPSULE NUMBER PER PLANT OF *OROBANCHE MINOR* SM.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 4 | 1 | 15 | 3 | 26 | 3 | 38 | 1 |
| 5 | 1 | 16 | 4 | 27 | 9 | 39 | 4 |
| 6 | 3 | 17 | 2 | 28 | 2 | 40 | 2 |
| 7 | 1 | 18 | 10 | 29 | 4 | 41 | 2 |
| 8 | 3 | 19 | 6 | 30 | 3 | 45 | 1 |
| 9 | 2 | 20 | 2 | 31 | 3 | 46 | 1 |
| 10 | 2 | 21 | 7 | 32 | 1 | 48 | 2 |
| 11 | 5 | 22 | 3 | 33 | 3 | 70 | 1 |
| 12 | 5 | 23 | 3 | 34 | 3 | 90 | 1 |
| 13 | 3 | 24 | 2 | 35 | 2 | | |
| 14 | 2 | 25 | 4 | 37 | 3 | | |

Total 2,976 capsules on 125 plants. Average 23·82±0·74.

TABLE XXXI (B). VARIATION IN CAPSULE NUMBER PER PLANT OF *OROBANCHE ELATIOR* SUTT.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 11 | 1 | 30 | 1 | 43 | 1 | 61 | 2 |
| 14 | 1 | 32 | 4 | 48 | 1 | 65 | 3 |
| 17 | 1 | 33 | 2 | 50 | 1 | 69 | 1 |
| 22 | 1 | 34 | 1 | 51 | 1 | 72 | 1 |
| 23 | 1 | 36 | 1 | 53 | 1 | 73 | 1 |
| 24 | 1 | 38 | 1 | 55 | 2 | 76 | 1 |
| 26 | 2 | 39 | 1 | 56 | 1 | 78 | 1 |
| 28 | 1 | 40 | 2 | 58 | 1 | 80 | 1 |
| 29 | 1 | 42 | 1 | 59 | 1 | 89 | 1 |

Total 2,094 capsules on 46 plants. Average 45·5±1·88.

TABLE XXXI (C). VARIATION IN CAPSULE NUMBER PER PLANT OF *OROBANCHE PICRIDIS* SCHULTZ.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 3 | 1 | 16 | 1 | 22 | 2 | 31 | 1 |
| 8 | 1 | 17 | 2 | 23 | 1 | 32 | 2 |
| 9 | 1 | 18 | 2 | 24 | 1 | 36 | 2 |
| 10 | 1 | 19 | 1 | 28 | 1 | 40 | 1 |
| 12 | 2 | 20 | 1 | 29 | 1 | 84 | 1 |
| 15 | 1 | 21 | 3 | 30 | 1 | | |

Total 726 capsules on 31 plants. Average 23·4±1·7.

TABLE XXXI (D). VARIATION IN CAPSULE NUMBER PER PLANT OF *OROBANCHE HEDERAE* DUBY.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 12 | 1 | 19 | 1 | 27 | 4 | 37 | 1 |
| 13 | 3 | 20 | 5 | 28 | 2 | 40 | 2 |
| 14 | 1 | 21 | 1 | 29 | 1 | 42 | 1 |
| 15 | 1 | 22 | 2 | 30 | 1 | 49 | 1 |
| 16 | 2 | 24 | 2 | 33 | 2 | | |
| 18 | 4 | 25 | 1 | 34 | 1 | | |

Total 972 capsules on 40 plants. Average 24·3±0·9.

Miss R. Dowling (1931) has called attention to a race of *O. minor* that appears to be restricted to *Plantago coronopus*. I have myself grown this strain from seeds sown in a mixed patch of Stag's-horn Plantain, *Plantago coronopus* and White Clover, *Trifolium repens*, but the Plantago was alone parasitized.

One large specimen, of this apparently specialized strain, bore 76 capsules, whilst others bore very few. Though the number of specimens examined is far too small to give any reliable average they suggest that the capsule production is similar to that of typical *O. minor*. The seeds were counted in five capsules, the numbers being 807, 844, 1,103, 1,120, and 1,177; an average of 1,010 seeds per capsule. The large specimen would therefore have borne some 76,000 seeds. If we accept Wentz's average of 1,500 seeds per capsule as typical for normal *O. minor* a large specimen would probably bear appreciably more seeds that the specialized strain. But in all probability there is little difference in their seed production capacity. The significant fact is that the evidence points to no augmentation of the seed production associated with the more specialized parasitism of a localized host.

*Orobanche Picridis* Schultz

I have only had the opportunity of examining two living British specimens of this rare species, one a specimen bearing 31 capsules and the other a very large plant which was parasitic upon a large specimen of *Dipsacus sylvestris* and bore 84 capsules. We can obviously regard this second specimen as an exceptionally large one, since it was just over 49 cm. high, and Coste (" Flore de France," 1906) gives the range of height for *O. Picridis* as from 10–50 cm. The seeds were counted in three average size capsules, and the numbers were 3,842, 4,272, and 4,378; a total of 12,492 seeds, or an average of 4,164 seeds per capsule. Thus, the large plant would have produced nearly 350,000 seeds. The data for fruit production was supplemented by examination of twenty-nine herbarium specimens (*cf.* Table XXXI (C) ), the average for the thirty-one specimens being 23·4±1·7 fruits per plant ($\sigma$ 14·24; S.E.M. 2·56). The average seed output would thus be between 94,000 and 116,000 seeds per plant. If, as has been suggested, this is a specialized sub-species of *O. minor* Sm. then these figures indicate that in this instance the biological specialization is

associated with a higher seed production. The average seed weight of this species (average of 3,000 seeds) is 0·0000029 gm.

*Orobanche elatior* Sutt.

Material of this species has been obtained from a number of localities. A large, well-grown specimen sent me by Mr. Dymes, from Baldock, bore sixty-nine capsules and the seeds counted in a single large capsule numbered two thousand five hundred and thirty-five. Thus, the total seed output from the plant would have been some 175,000 seeds. A second specimen bore forty-three capsules, and a typical capsule was found to contain 3,389 seeds, which indicates a seed output of about one hundred and forty-five thousand.

Some very fine specimens sent me from near Devizes by Mr. Marsden-Jones bore respectively eighty-nine, fifty-nine, fifty-six, and forty-eight capsules. An average well-developed capsule from the largest of these specimens contained 2,981 seeds, so that its seed production would probably be between 260,000 and 270,000 seeds.

Nine large specimens growing on a specially luxuriant plant of *Centaurea Scabiosa*, which had been carefully cultivated for the purpose in my own garden before the seeds of the parasite were sown around it, bore respectively 38, 42, 55, 58, 61, 65, 65, 73, and 80 capsules. Two apparently average capsules from two of these plants contained only 1,136 and 826 seeds.

Other plants from various localities were only examined for the number of fruits produced. A total of forty-six plants (*cf.* Table XXXI (B) ) bore 2,094 capsules, or an average of $45{\cdot}5 \pm 1{\cdot}88$ ($\sigma$ 19·1; S.E.M. 2·8).

The individual seeds weigh only 0·0000049 gm., and this, combined with the fact that aborted seeds and unfertilized ovules may occur in considerable numbers in some of the capsules, render direct counting under a 1-in. objective the only really satisfactory method of determining the number of seeds per capsule. Although only five capsules were examined in this way it involved the careful examination and counting of nearly 11,000 seeds. In order, however, to obviate to some extent the necessary limitation on the numbers of capsules examined the entire contents of 45 capsules were gone over with a dissecting microscope to remove obvious organic debris, although no attempt was made to remove abortive ovules as when the careful counts were made. The total weight was then determined and the number of seeds estimated on the basis of comparison with 2,200 seeds which had been carefully separated out and weighed. The average number of seeds thus obtained for the 45 capsules was 2,130 seeds per capsule. This is not far below the average of 2,175 for the contents of the five capsules actually counted. The weighing method might have been expected to yield the higher value for the reasons already mentioned, but three out of the five capsules from which the seeds were counted had been obtained from very large plants, the average size of the capsules on which might well have exceeded the normal. Probably we shall not greatly err if we assume that the average seed content of a capsule in this species is about two thousand one hundred and fifty. This, in round figures, gives an average seed output per plant of between 94,000 and 102,000 seeds.

Whilst no exact data can be furnished respecting the germinative capacity of the seeds of *Orobanche*, from the results of experiments carried out by the author on *O. elatior* in which seeds of this species were sown around plants of *Centaurea Scabiosa*, it would appear that either there is a very low percentage germination or that there is a very high seedling mortality before any signs of the parasite appear above ground.

*Orobanche Hederae* Duby.

Forty plants of this species bore from 12 to 49 capsules, with an average of 24 capsules ($24{\cdot}3 \pm 0{\cdot}9$. $\sigma$ 8·8; S.E.M. 1·4). The number of seeds per capsule in this species is probably lower than in those previously considered, since the few capsules examined indicated an average of only 1,040.

*Orobanche variegata* Wallr.

Although not a British species this is of interest as parasitizing woody leguminous plants in the Mediterranean region. I am indebted to Mrs. E. S. Russell for kindly obtaining for me fruiting specimens from Collioure (Pyrenees Orientale). Well-grown specimens had up to 53 capsules. The seeds were counted in several capsules and ranged from 1,800 to 2,000, so that a vigorous plant would bear under 100,000 seeds. Probably rather less, as in some of the capsules the number of obviously infertile seeds was rather high. However, the chief interest of the data for this species, from the region where so many species of this genus flourish, is that the seed production is of the same order as that of the British specimens investigated, so that although the genus *Orobanche* approaches its northern limit in this country there is no reason to assume that the seed production is impaired for that reason.

Summarizing our information for this genus we have the following approximate seed productions:

| | Average | Very large specimens |
|---|---|---|
| Orobanche minor | 35,000 seeds | 135,000 seeds |
| Orobanche minor biological strain on P. coronopus | | 75,000 ,, |
| Orobanche picridis | 105,000 ,, | 350,000 ,, |
| Orobanche elatior | 98,000 ,, | 270,000 ,, |
| Orobanche Hederae | ? 25,000 ,, | |
| Orobanche variegata | 100,000 ,, | |

Thus, although it be true that the seed production of the Broomrapes is large it is by no means conspicuously so, having regard to all the circumstances and in comparison with non-parasitic species of the Scrophulariaceae. It is naturally not easy to decide what species should most appropriately be chosen for such comparison. Preferably the non-parasitic species should be ones having seeds of similar weight, and the size of the plants similar to that of the host-plants to which the *Orobanche* is attached. Thus it is not unjustifiable to compare the seed production of the *O. picridis* growing on a large Teazle with that of a well-grown Foxglove, although since the seeds of the latter are eighteen times heavier than the seeds of the Broomrape such comparison is to the disadvantage of the Foxglove. Yet despite the discrepancy of seed

weight large plants of *Digitalis purpurea* will produce from 100,000 to over 500,000 seeds. Further, the germination of these seeds in light is often nearly 100 per cent.

A nearer approach to the same seed weight as that of *Orobanche* in plants which are neither parasites nor saprophytes is furnished by *Orchis maculata*, which is also suitable as being a constituent of the chalk flora, like *O. elatior*, and from its high frequency and widespread occurrence it is evident that, compared with the Broomrape, the risks of the seeds being blown to an unsuitable locus are far less. The seed output of the terrestrial Orchids will be considered from this aspect in a subsequent section.

Toothwort, *Lathraea squamaria* L.

The host plants of *Lathraea squamaria* are rather varied, but the most usual are *Corylus avellana* and *Ulmus montana*. It is primarily a species of the Oak Hazel woods on the more basic types of soil where Hazel is abundant and where alone the Toothwort is of frequent occurrence. It is, however, always local in its distribution. Its chief interest for the present consideration is that, unlike most parasites, it has seeds which are relatively heavy, the average weight being 0·000532 gm.

In the six plants examined the number of fruits ranged from 24 to 200, with an average of 93 fruits per plant. The seeds were counted in fifteen capsules, and ranged from 73 to 110, with an average of 83·4 seeds per capsule. The seed production per plant therefore averaged 7,756, whilst that of the largest plant would have been about sixteen thousand seven hundred. Although the seed output is thus low it may be noted that the total weight of seeds per plant would average about 4 gm. compared with 0·6174 gm. for the total weight of the average seed output of *O. elatior*. Since the Toothwort is a woodland plant its heavy seeds suggests the possibility that its complete parasitism may be phylogenetically recent.

## The Seed Production of Semi-Parasites

In general, it may be said that the semi-parasites are comparable to unspecialized parasites, and since most attach themselves to grasses there must be comparatively little risk of the seeds not being shed near a suitable host. Moreover, they are capable of independent existence under suitable conditions though they rarely attain any appreciable vigour under such circumstances. As the sequel will show, they present a striking range both with respect to the number of seeds produced in the capsules and also as regards the weight of the individual seeds.

## The Genus Bartsia

Three species of this genus have been examined, namely *Bartsia Odontites*, which is both widespread and abundant, *Bartsia viscosa*, a Southern-Oceanic species with a rather restricted western distribution and decidedly local in occurrence (*cf.* Salisbury (1938), *Jour. Bot.*, p. 68), though in suitable situations the number of individuals may be large, and *Bartsia alpina*, an arctic-alpine

species of very local occurrence. The respective comital and vice-comital frequencies (percentages) are as follows:

| | England | Scotland | Ireland | British Isles |
|---|---|---|---|---|
| Bartsia odontites | 100 | 97·5 | 100 | 99·3 |
| Bartsia viscosa | 28·1 | 17·0 | 20 | 23·0 |
| Bartsia alpina | 5·6 | 4·9 | — | 3·3 |

*Bartsia Odontites* Huds., Common Red Bartsia

The range in size of individual plants is considerable. The largest specimen examined bore 445 capsules and the smallest nine. The capsules were counted on 124 specimens and totalled 13,903, or an average of 112 capsules per plant (112±4·8). The standard deviation was 79·9 and the standard error of the mean 7·2.

The seeds were counted in one hundred and twenty capsules, for which the details are furnished in the accompanying Table XXXII.

TABLE XXXII. VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *BARTSIA ODONTITES* Huds.

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 10 | 5 | 19 | 5 | 28 | – |
| 2 | 2 | 11 | 6 | 20 | 6 | 29 | – |
| 3 | 0 | 12 | 7 | 21 | 0 | 30 | – |
| 4 | 2 | 13 | 14 | 22 | 4 | 31 | 1 |
| 5 | 1 | 14 | 13 | 23 | 4 | 32 | – |
| 6 | 1 | 15 | 12 | 24 | 2 | 33 | – |
| 7 | 4 | 16 | 6 | 25 | 2 | 34 | – |
| 8 | 3 | 17 | 6 | 26 | 1 | 35 | – |
| 9 | 4 | 18 | 6 | 27 | 1 | 36 | 1 |

Total 120 capsules. Average 14·8 seeds/capsule. $\sigma = 5{\cdot}7$. S.E.M. 0·52.

The number of seeds in each capsule is thus seen to range from one to thirty-six, with an average of approximately fifteen (14·8±0·34). The standard deviation is 5·7 and the standard error of the mean 0·52.

The average seed output is therefore approximately 1,660±105 seeds, and even that of the largest individuals is only about 6,600 seeds. The average weight of the individual seeds is 0·0001 gm., so that the average weight of reproductive bodies per plant is 0·239 gm. per plant.

*Bartsia viscosa* L., Yellow Bartsia

Here also the range is very considerable, as is shown in the following Table XXXIII. The range observed in 172 plants was from two capsules to eighty-six capsules. The average number is twenty-one (21·3±0·7), whilst the mode would appear to be lower. The seeds were counted in twenty-three capsules. They varied in number from 166 to 483, as follows: 166, 230, 243, 274, 299, 303, 304, 310, 314, 326, 337, 340, 342, 345, 367, 372, 380, 382,

383, 414, 440, 442, 483. The average number was 339±9·8 seeds per capsule, with a standard deviation of 70·8 and a standard error of the mean of 14·7. The average number of seeds per plant was therefore about 7,227±446. It should be noted that in this species the seeds are much smaller than in *B. Odontites* and weigh only 0·000021 gm. each. The largest plant encountered would produce over 28,000 seeds, or rather more than four times the quantity from the largest plant of *B. Odontites*. The average weight of seed per plant is 0·1518 gm., or about 38 per cent less than that of *B. Odontites*.

TABLE XXXIII. VARIATION IN NUMBER OF CAPSULES PER PLANT OF *BARTSIA VISCOSA* L.

| Capsules per plant | Number of plants | Capsules per plant | Number of plants | Capsules per plant | Number of plants | Capsules per plant | Number of plants |
|---|---|---|---|---|---|---|---|
| 1 | 0 | 14 | 6 | 27 | 4 | 45 | 1 |
| 2 | 1 | 15 | 6 | 28 | 1 | 46 | 1 |
| 3 | 2 | 16 | 4 | 29 | 3 | 48 | 1 |
| 4 | 0 | 17 | 8 | 30 | 2 | 51 | 1 |
| 5 | 1 | 18 | 5 | 31 | 4 | 54 | 3 |
| 6 | 4 | 19 | 6 | 32 | 2 | 58 | 1 |
| 7 | 5 | 20 | 4 | 33 | 4 | 65 | 1 |
| 8 | 8 | 21 | 5 | 34 | 2 | 66 | 1 |
| 9 | 6 | 22 | 5 | 35 | 1 | 79 | 1 |
| 10 | 8 | 23 | 5 | 36 | 4 | 86 | 1 |
| 11 | 9 | 24 | 6 | 37 | 3 | | |
| 12 | 8 | 25 | 2 | 38 | 3 | | |
| 13 | **10** | 26 | 1 | 42 | 2 | | |

Total 172 plants, 3,667 capsules. Average 21·3 capsules per plant ±0·7. Standard deviation 13·9. Standard error of mean 1·06.

*Bartsia alpina* L., Mountain Bartsia

A total of thirty-five plants were examined and yielded from four to nineteen capsules with an average of approximately six per plant (5·9±0·04). The mode was four capsules. Eleven plants, or 31·4 per cent, bore this number. The standard deviation was 3·33 and the standard error of the mean 0·056. The seeds were counted in twenty-five capsules and varied in number from twelve to sixty as follows: 12, 18, 20, 27, 29 (2), 34 (2), 35, 37, 38, 40 (3), 43, 45, 46, 47, 51, 52, 53 (2), 57, 60. Thus there is a suggestion of a mode of forty seeds. The average number was about forty (39·7±1·62). The standard deviation was 12·2 and the standard error of the mean 2·44. The average seed output was therefore about 234±11 seeds. The seeds are heavier than those of *B. viscosa* but less so than *B. Odontites*. The average weight of some seeds from Teesdale was 0·00011 gm. Porsild, however, gives higher weights, viz. 0·000191 gm. and 0·0002066 gm. for the averages of two separate batches of 300 seeds. Taking the mean value of all three determinations, viz. 0·000169 gm., the average weight of seed produced by a plant of *Bartsia alpina* would be 0·0395 gm. as compared with 0·15 gm. for *B. viscosa* and 0·24 gm. for *B. Odontites*. All three species occur in semi-closed grassland

communities. *B. alpina* and *B. viscosa* frequent damper situations, the latter especially growing in taller herbage than the other species. As they are photosynthetic plants the shade of the surrounding vegetation will influence their early development, so that seed weight as well as number is a pertinent consideration in their establishment. It is probably, therefore, significant that the order of frequency and abundance of *B. alpina*, *B. viscosa*, and *B. Odontites* (which as judged by the comital and vice-comital frequency approximates to 1 : 4 : 6) corresponds with that of the weights of their average seed outputs (which approximate respectively to 1 : 7 : 30). The ratios of the average seed output have a different order, namely 1 : 30 : 7. No exact estimate can be given of their respective reproductive capacities as few germination data are available; but whereas the germination of *B. Odontites* is certainly high that of *B. alpina* is unquestionably low. Kinzel, indeed, gives 8 per cent only for this species. From data supplied me by Miss Joan Ivimy and Mrs. Steen, who are investigating the ecology of *B. viscosa*, the percentage germination of this species, in light, would appear to be intermediate. So we are probably safe in stating that the reproductive capacities of the three species would probably exhibit the same sequence as the weights of seed per plant but in an accentuated form.

*Pedicularis palustris* L., Red Rattle

The number of capsules was determined for only a few specimens but ranged from 27 to 400 per plant with an average of 165 capsules. The seeds are relatively heavy, the mean weight, according to Dallman (1933), being 0·00075 gm. The contents of thirty capsules showed the following range:

TABLE XXXIV. VARIATION IN SEED NUMBER PER CAPSULE OF RED RATTLE, *PEDICULARIS PALUSTRIS* L.

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|
| 6 | 1 | 14 | 4 |
| 7 | 1 | 15 | 2 |
| 8 | 1 | 16 | 0 |
| 9 | 1 | 17 | 2 |
| 10 | 3 | 18 | 0 |
| 11 | 4 | 19 | 1 |
| 12 | 8 | 20 | 1 |
| 13 | 1 | | |

Total 372 seeds in 30 capsules.

The average number of seeds per capsule is twelve ($12{\cdot}4 \pm 0{\cdot}38$; $\sigma$ 3·16; S.E.M. 0·57). The seed output would therefore be about 1,980 seeds per plant and the average weight of seeds 1·48 gm. per plant.

*Melampyrum pratense V. Hians* Druce, Cow Wheat

Sixty plants of this species of upland woods were examined; the number of capsules which they produced varied from two to one hundred and twenty-five. The average was twenty-five ($24{\cdot}73 \pm 1{\cdot}9$) capsules per plant, with a standard deviation of 21·6 and a standard error of the mean of 2·8.

The seeds were counted in 366 capsules and showed the following variation:

| | | |
|---|---|---|
| 1 seed per capsule | | 17 capsules |
| 2 seeds | ,, | 138 ,, |
| 3 seeds | ,, | 135 ,, |
| 4 seeds | ,, | 76 ,, |

The average is thus $2{\cdot}73 \pm 0{\cdot}029$ seeds per capsule, with a standard deviation of 0·83 and a standard error of the mean of 0·043.

The average seed output is therefore sixty-seven per plant $\pm 5{\cdot}9$. The average weight of the seed was 0·00646 gm., so that the average seed output would weigh 0·43 gm.

It is of interest to note that the seeds of these woodland semi-parasites are in general heavier than those of species characteristic of the open meadow. A number of seeds of *Melampyrum cristatum*, for instance, yielded an average weight of 0·00975 gm.

*Rhinanthus* (*crista-galli* L.) *minor* Ehrh., Yellow Rattle

This species is a familiar feature of poor pastures, where the herbage is of a semi-closed character. But the fact that it sometimes occurs on better soils, where, owing to browsing, the herbage is short suggests that it is the competition factor that is responsible for its absence from the more lush types of grassland. One hundred and seventy-one plants were examined for capsule production, the details of which are furnished in Table XXXV.

TABLE XXXV. VARIATION IN FRUIT PRODUCTION OF YELLOW RATTLE, *RHINANTHUS* (*CRISTA-GALLI* L.) *MINOR* EHRN.

| Fruits per plant | Number of individuals | Fruits per plant | Number of individuals | Fruits per plant | Number of individuals | Fruits per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 2 | 3 | 15 | 0 | 28 | 4 | 41 | 0 |
| 3 | 3 | 16 | 4 | 29 | 0 | 42 | 1 |
| 4 | 9 | 17 | 5 | 30 | 3 | 43 | 1 |
| 5 | 15 | 18 | 3 | 31 | 2 | 44 | 1 |
| 6 | 15 | 19 | 3 | 32 | 3 | 45 | 0 |
| 7 | 8 | 20 | 3 | 33 | 1 | 46 | 1 |
| 8 | 6 | 21 | 0 | 34 | 1 | 47 | 1 |
| 9 | 14 | 22 | 3 | 35 | 3 | 48 | 1 |
| 10 | 7 | 23 | 1 | 36 | 1 | 49 | 1 |
| 11 | 11 | 24 | 2 | 37 | 0 | 50 | 1 |
| 12 | 3 | 25 | 4 | 38 | 0 | 61 | 1 |
| 13 | 3 | 26 | 3 | 39 | 3 | 68 | 1 |
| 14 | 6 | 27 | 3 | 40 | 2 | 193 | 1 |

**Total 2,970 capsules on 171 plants. Average $17{\cdot}3 \pm 0{\cdot}96$. $\sigma$ 18·8 ; S.E.M. 1·44.**

It will be seen that the mean number of fruits per plant is $17{\cdot}3 \pm 0{\cdot}96$ ($\sigma = 18{\cdot}8$; S.E.M. 1·44). The variation in number of seeds in the individual capsules is shown in Table XXXVI for 250 capsules. The average is $9{\cdot}7 \pm 0{\cdot}1$.

TABLE XXXVI. VARIATION IN SEED NUMBER PER CAPSULE OF *RHINANTHUS (CRISTA-GALLI* L.) *MINOR* EHRH.

| Number of seeds per capsule | Number of capsules | Number of seeds per capsule | Number of capsules |
|---|---|---|---|
| 1 | 0 | 9 | 34 |
| 2 | 1 | 10 | 37 |
| 3 | 2 | 11 | 47 |
| 4 | 2 | 12 | 31 |
| 5 | 7 | 13 | 16 |
| 6 | 12 | 14 | 6 |
| 7 | 17 | 15 | 3 |
| 8 | 34 | 16 | 1 |

Total 2,432 seeds from 250 capsules. Average 9·7 seeds per capsule. $\sigma$ 2·40. Standard error of mean 0·15.

The average seed output is therefore $168 \pm 11$ seeds per plant.

Our consideration of these semi-parasites, therefore, shows in general a rather low seed production except that of *Bartsia viscosa*. It would not therefore appear that the production of a large seed output is in any sense a necessary concomitant of the semi-parasitic habit. Indeed, the example of *B. viscosa* points clearly to the conclusion that the seed production in these plants is markedly correlated in a negative manner with the seed size. In the complete parasites the extremely minute seeds are rendered possible without detriment by a mode of nutrition that evades photosynthesis, but as this is not the condition in the semi-parasites it is scarcely surprising that the seeds of the woodland types are relatively heavy. It may well be that the seeds of *Lathraea squamaria* are also relatively heavy, for a totally parasitic species, by reason of specialization in respect to the greater depth of the root systems of its arboreal hosts as compared with those normally attacked by species of *Orobanche*. The fact that *Lathraea* is itself a woodland plant would only be significant in this connection if its woodland habit was an ancestral character that antedated the assumption of the completely parasitic mode of life. A large number of small seeds which will become widely scattered are not merely a necessity for the survival of the specialized parasite but ensure that an appreciable proportion of the very scattered ecological niches which can support them are in fact occupied. For them the large seed output is, indeed, in considerable measure an insurance against the mortality risks, but these, unlike those to which many plants are subject, are mainly risks of position. In this sense they conform to the same governing factor shown by plants which have no such specialized requirements but which produce large seed outputs. It is, in other words, a positive asset that tends towards extension and not merely the maintenance of the *status quo*. The more scattered and restricted the habitats of a species or the more specialized a parasite the more nearly the seed output will approximate to the requisite insurance against non-survival.

## THE SEED OUTPUT OF SAPROPHYTES AND SEMI-SAPROPHYTES

### *Monotropa hypopitys* L., Bird's Nest

The seeds of this complete saprophyte have an average weight of 0·000003 gm. The contents of two average-sized capsules were counted. The first contained

1,953 seeds and the second 1,980, so that we shall probably not be far wrong in assuming that the average number of seeds per capsule is about 1,970 seeds.

The number of capsules borne on a plant usually ranges from four to twelve, and the average number as well as the mode for a number of plants examined was eight (S.E.M. 1·1). The average seed output would therefore be about sixteen thousand.

H. L. Francke found that the seeds failed to germinate in the absence of the symbiotic fungus, but even in its presence he only obtained from 0·3 to 0·5 per cent (Flora, 1935). If then these germination figures are in any sense representative the reproductive capacity would appear to be about 50 to 80 per plant. This is an extremely low reproductive capacity, especially having regard to the rather localized and patchy character of the conditions requisite for the growth of this plant. The large number of seeds probably is, indeed, responsible in no small degree for the low viability, since, as Francke showed, they contain an embryo of only three cells and an endosperm of only nine! Here, then, as in the parasites previously considered, the large seed output is probably less advantageous than a smaller number of larger seeds as an insurance against reproductive failure, but is advantageous as assuring more efficient dispersal and thus facilitating the colonization of the very scattered suitable loci.

The striking fluctuations in the number of inflorescences in a given locality in different seasons suggests that the population of *Monotropa hypopitys* may be subject to similar variation. If so, then the Bird's nest is akin to the species of intermittent habitats which, as will be shown later, are characterized by large seed outputs.

## PYROLA SPECIES, WINTERGREEN

The members of this genus can be regarded as semi-saprophytes. Though capable of photosynthesis they require habitats with a high humus content and can endure deep shade. All the species agree in possessing very small, light seeds. They are comparable to those of the terrestrial orchids but with a smaller central region containing the actual embryo (*cf.* Fig. 21). All the pyrolas possess mycorrhiza, but Christoph (1921) was unable to find any direct relation between fungal infection and seedling development. But the fact that he only obtained germination of the seeds on sterilized soil when organic solutions had been added suggests that even if the association be not of an obligate character the fungus, if present, assists in the saprophytism of the seedling and may well compensate for the diminutive food reserve. It is significant that Christoph found darkness (and high humidity) conducive to the best germination and records up to more than 75 per cent germination for *Pyrola rotundifolia.*

### *Pyrola secunda* L.

Forty-five infructescences showed a range in number of capsules from nine to fourteen, as follows: Eight capsules (3); 9 capsules (5); 10 capsules (8); 11 capsules (8); 12 capsules (11); 13 capsules (9); 14 capsules (1). The average is thus $11{\cdot}1 \pm 0{\cdot}15$ capsules ($\sigma$ 1·57; S.E.M. 0·23). The contents of six capsules were counted, the numbers of seeds being 147, 157, 236, 371,

490, and 515. Thus the average seed number in a capsule is 320 (standard deviation 148·9; S.E.M. 62). The average seed output for *Pyrola secunda* is therefore probably about 3,558±503 seeds per inflorescence. Actually *P. secunda* has a branched rhizome and each plant bears several inflorescences. In the other species there is a similar branching, but the underground connection between the leafy rosettes does not usually persist. From the point of view of the relative capacities for seed production within the genus the difference is more theoretical than practical, and it will be best to compare the seed output per inflorescence. For comparison with other plants, however,

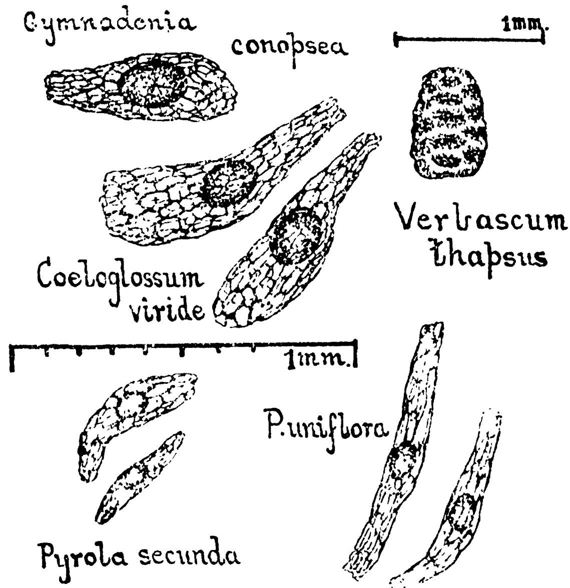



FIG. 21. SEEDS OF ORCHIDS AND WINTERGREEN. A seed of the Sweet-scented Orchis (*Gymnadenia conopsea*) and two seeds of the Frog Orchis (*Coeloglossum viride*) are shown above and, on the same scale (×45) below, seeds of *Pyrola secunda* and *P. uniflora*. Above on the right is shown a seed of the Mullein (*Verbascum thapsus*) on a smaller scale (×20).

the seed production per inflorescence should be multiplied by from 3 to five. It must nevertheless be recognized that where a species exhibits any appreciable vegetative spread the unit of reproduction should not be the so-called "individual" or separated clone but rather the seed production per unit area should be the basis for comparison. This is manifestly so for such species as *Anemone nemorosa*, *Adoxa moschatellina*, which frequently occur in almost pure stands, but cannot satisfactorily be applied to the large number of species that grow intermingled with others.

*Pyrola media* Sw.

Twenty-four plants of this species showed a range of from four to twelve capsules per plant. The mode was nine or ten capsules and the average

$8{\cdot}75 \pm 0{\cdot}33$ capsules per plant ($\sigma$ 2·4; S.E.M. 0·49). The seeds were counted in seven capsules, the numbers being 330, 515, 1,200, 1,230, 1,737, 1,897, and 2,742 seeds respectively. The average was thus 1,379 seeds per capsule $\pm 197$ (standard deviation 770; S.E.M. 296). So that the real mean is probably between 1,182 and 1,576 seeds per capsule. Thus, the seed output probably has a mean value of between about 10,000 and 14,000 seeds per plant.

*Pyrola uniflora* L.

In this species, where there is but a single flower and therefore but one capsule, it is scarcely surprising to find that the seed production per capsule is much greater. Owing to the very large number of seeds and the difficulty of counting them the exact number was only ascertained in two capsules, both of which were chosen as being of apparently average size. The first contained 4,000 and the second 4,762 seeds. The seed production per fruit is thus very high, but having regard to the special conditions that the species demands, and its rarity, the seed production per plant may be regarded as low.

The genus *Pyrola* thus illustrates the potentiality for minute seed production in a semi-saprophytic group; but the output is rather small, having regard to the risks attendant upon their dispersal by wind of not reaching a suitable nidus.

*Goodyera repens* Br.

This Orchid has very much the same type of habitat as *Pyrola secunda*, and, like that species, is a semi-saprophyte often found in situations of low light intensity.

A single plant will produce from one to twelve inflorescences. The capsules were counted on 130 infructescences, with the following results:

TABLE XXXVII

| Number of capsules | Number of specimens | Number of capsules | Number of specimens |
|---|---|---|---|
| 6 | 3 | 17 | 15 |
| 7 | 2 | 18 | 13 |
| 8 | 5 | 19 | 7 |
| 9 | 7 | 20 | 3 |
| 10 | 6 | 21 | 4 |
| 11 | 9 | 22 | 4 |
| 12 | 8 | 23 | 0 |
| 13 | 12 | 24 | 1 |
| 14 | 8 | 25 | 2 |
| 15 | 9 | 26 | 1 |
| 16 | 9 | 31 | 1 |

Average 14·8 capsules per infructescence.

The average number of capsules was therefore $14{\cdot}8 \pm 0{\cdot}26$ ($\sigma$ 4·5; S.E.M. 0·39).

The smallest capsules at the top of the inflorescences contained between 300 and 400 seeds, whilst the largest capsules examined contained about 4,000, the average of all counts being 1,700 seeds per capsule. If we assume the average number of inflorescences per plant to be six then the average seed output is about 150,000 seeds per plant. According to Kerner the weight of

the seed is 0·000002 gm., so that the weight of the average output would be about a third of a gram (0·306 gm.).

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It is evident, then, that so far as the semi-saprophytes are concerned they may or may not have large outputs of seed but they agree with the complete saprophytes and some parasites in one feature, namely the small size of their seeds, which here again is rendered possible without undue detriment to the chances of survival by reason of the mode of nutrition. They may be said to exhibit a high degree of efficiency with respect to the distribution of their seeds at the sacrifice of efficiency for establishment since the minute provision of food reserve and the lack of differentiation in the embryo necessarily implies a smaller margin of safety against the risks of mortality in the earliest stages of development.

# XI

# THE REPRODUCTIVE CAPACITY OF TERRESTRIAL ORCHIDS

No attempt has been made to investigate the seed output of the Orchids intensively. All that has been aimed at is an approximate estimate of their seed production for comparison, with the parasitic plants with seeds of similar weight, on the one hand, and on the other with the species to be dealt with later which are more definitely associated with habitat conditions that are intermittently available and to which class some of these terrestrial orchids may also belong.

Spotted Orchis, *Orchis maculata* L. (*O. Fuchsii* Druce)

The capsules produced by 33 plants from several localities ranged from six to thirty-eight, with a mean of 17 capsules per plant. The standard deviation was 8·5 and the standard error of the mean 1·49.

Darwin estimated the number of seeds in a single capsule of this species as 6,200 seeds, but the method he adopted was not likely to yield very accurate results. I have myself counted the seeds carefully in four capsules, which, so far as one could judge, were of average size. These yielded 2,199, 3,378, 3,600, and 4,000 seeds respectively. The average was therefore 3,294, and hence, on the basis of seventeen capsules per plant, the mean seed output would be just about 56,000 per plant. This is over one and a half times that estimated for *Orobanche minor* but only about one-half of that estimated for *Orobanche picridis*. But it cannot be maintained that the risks of the seeds of *Orchis maculata* reaching unsuitable locations are anything like those which the Broomrape has to surmount, and, indeed, having regard to all the circumstances, we are not only justified in denying the statement made by Professor Buckman regarding the Broomrapes (Lindley and Moor, 1874, p. 842) that " perhaps few plants produce more seed " but also in asserting that the seed output of *Orobanche* is appreciably lower than might be anticipated, having regard to the attendant risks. Furthermore, it must be remembered that probably the Broomrapes are monocarpic plants whereas *O. maculata* is a polycarpic species, with a life span of certainly over ten years, so that the seed production during its period of maturity is probably between 750,000 and 1,000,000 seeds, of which the percentage germination would appear to be high.

Green-Winged Orchis, *Orchis Morio* L.

Twenty-four fruiting specimens of this Orchis yielded a range of from three to thirteen capsules with an average of $7{\cdot}6 \pm 0{\cdot}39$ capsules per plant (3 (3), 4 (1), 5 (3), 6 (1), 7 (2), 8 (5), 9 (3), 10 (2), 11 (1), 12 (2), 13 (1)).

These data suggest a mode of eight capsules so that we may probably take that number as likely to correspond to the average for a larger sample. Only

one capsule was examined for seed number and this was over four thousand. It is probable then that the average output of seed is of the order of 32,000 per plant. This orchis is frequently found in flower in large numbers in areas where specimens had not been seen in previous years and no living plants may be found in the following seasons. It is very probable then that this species is monocarpic and not unlikely that the conditions which are favourable for its growth only obtain intermittently.

Pyramidal Orchis, *Orchis pyramidalis* L. (*Anacamptis pyramidalis* Rich.)

The number of capsules per plant in the specimens examined ranged from one to thirty-nine, with an average of about eighteen. The seeds were only counted in a single capsule and numbered one thousand nine hundred and thirty-five. These figures suggest an average output of about 35.000 seeds per plant. The very marked fluctuations in the flowering population of this species may again indicate a monocarpic tendency.

Bee Orchis, *Ophrys apifera* Huds.

If we consider the Bee Orchid as a monocarpic species, which is the condition for the great majority of individuals, though a few fruit a second year or rarely even a third, the comparison with *Orobanche* is clearly more valid. The number of capsules in *Ophrys apifera* ranges from one to nine on a plant, with a mean of four capsules. I have counted the seed contents of two normal-sized capsules: in the one the number was just over 8,000 seeds and in the other nearly 9,000, while in another very large capsule there were 26,500 seeds, so that probably the average number is about ten thousand. This gives an estimated seed output of 40,000, or over one-third of that for an average plant of *Orobanche elatior*. When we recall the size of the host plant of this Broomrape in comparison with the assimilatory surface presented by *O. apifera* one has to admit that the seed production of the latter is proportionately greater.

Fly Orchis, *Ophrys muscifera* Huds.

The observations of Detto in the years 1903 and 1904 showed that of 2,436 flowers of this species only 108 set fruit, *i.e.* 4·4 per cent. This failure to set fruit appears to be general, and the relatively sparse occurrence of this species may well be connected with a low reproductive capacity.

Fragrant Orchis, *Gymnadenia conopsea* (L.) R. Br.

The " Fragrant Orchis " is a locally common species, but, as mentioned in the " Flora of Sussex " (A. H. Wolley-Dod, 1937, p. 433), " it varies considerably in its numbers in the same station from year to year," and " in places where it is said to be common there are years in which hardly a single specimen can be seen." Such statements, which agree with my own experience, suggest that *Gymnadenia conopsea* is either a short-lived perennial or perhaps frequently monocarpic.

The uppermost flowers frequently do not set seed, and probably nutritional factors are mainly responsible for the difference between the number of

flowers on the spike and the number of capsules formed, although the occasionally interrupted arrangement of the capsules is presumptive evidence of irregular pollination. The capsules were counted on one hundred and fifty-nine fruiting specimens, which showed the following distribution:

TABLE XXXVIII. VARIATION IN NUMBER OF MATURE CAPSULES OF *GYMNADENIA CONOPSEA* R. BR.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 2 | 1 | 11 | 11 | 21 | 5 | 31 | 1 |
| 3 | 0 | 12 | 9 | 22 | 4 | 32 | 1 |
| 4 | 4 | 13 | 7 | 23 | 3 | 33 | 1 |
| 5 | 5 | 15 | 8 | 24 | 3 | 34 | 1 |
| 6 | 7 | 16 | 10 | 25 | 0 | 35 | 2 |
| 7 | 5 | 17 | 4 | 26 | 5 | 36 | 2 |
| 8 | 12 | 18 | 7 | 28 | 3 | 39 | 1 |
| 9 | 9 | 19 | 4 | 29 | 3 | 43 | 1 |
| 10 | 9 | 20 | 4 | 30 | 0 | | |

Total 159 plants 2,450 capsules.

The average number of capsules was thus 15·4±0·43 ($\sigma$ 8·2; S.E.M.0· 65). The seeds were only counted in three capsules, namely a small one which contained 911 seeds, one of medium size which contained 1,260 seeds, and one large capsule which contained 3,960 seeds, an average of 2,044±515. Thus the average output of seeds per plant would be 31,699±8,809. or between 23,000 and 40,000 seeds.

Frog Orchis, *Coeloglossum viride* (L.) Hartm. (*Habenaria viridis* R. Br.)

This is a species very erratic in its occurrence and possibly often monocarpic. The capsules formed on forty-four specimens were as follows: 2 (1), 3 (1), 4 (4), 5 (2), 6 (5), 7 (3), 8 (7), 9 (4), 10 (2), 11 (4), 12 (3), 13 (3), 14 (1), 15 (2), 18 (1), 20 (1). A total of 395 capsules, or an average of 9·0±0·38 capsules per plant ($\sigma$ 3·8; S.E.M. 0·57). The seeds were counted in four capsules and numbered 690, 930, 1,485, and 2,251, an average of 1,330±156. These data indicate an average output of about 12,000 seeds per plant (12,028±1,909).

Butterfly Orchis, *Habenaria chlorantha* Bab.

The number of capsules would appear to range from one to eleven with an average of 5·5±0·78. The seeds were counted in only one capsule and numbered 2,500. This would indicate an output of about 13,750 seeds per plant per annum.

*Listera ovata* (L.) Br.

The capsules formed were counted on twenty-nine plants and ranged in number from 18 to seventy-one. The average number was thirty-nine (38·7 ±1·6; $\sigma$ 13·8; S.E.M. 2·5).

The seeds in three capsules numbered respectively 382, 442, and 807, an

average of five hundred and forty-four. These data then would indicate an average seed output of between 20,000 and 22,000 per plant. It should, however, be mentioned that the seed contents were determined in an unfavourable season for this species, so that the seed numbers may be below the normal. *Listera ovata* is a polycarpic type and the same individual will fruit over a period of at least several years.

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If we summarize the data obtained for the terrestrial Orchids investigated and consider them in relation to their comital frequencies in Britain, we are at once struck by the widespread distribution of all of them in England and Ireland.

| Species | Average output of seeds/plant | Comital frequencies (percentages) England | Scotland | Ireland |
|---|---|---|---|---|
| Orchis maculata | 56,000 | 96 | 97 | 90 |
| Ophrys apifera | 40,000 | 87·3 | 2·4 | 85 |
| Orchis pyramidalis | 35,000 ? | 88·7 | 14·6 | 100 |
| Orchis Morio | 32,000 ? | 94·3 | 0 | 55 |
| Gymnadenia conopsea | 32,000 | 97 | 87·8 | 95 |
| Listera ovata | 21,000 ? | 100 | 100 | 100 |
| Habenaria chlorantha | 13,750 ? | 87 | 80 | 100 |
| Coeloglossum viride | 12,000 | 90 | 100 | 100 |

It will be evident that, apart from the Frog Orchis and the Butterfly Orchis, and the doubtful exception of the Twayblade, of which the seed production may well be appreciably higher, the output of seeds of these Orchids is of about the same order of magnitude. The outputs of *Coeloglossum viride* and *Habenaria chlorantha* are noteworthy as being so much lower than the others and as being the sole examples amongst these Orchids which, though also of high frequency are of relatively low abundance. Thus, in the counties of Kent, Surrey, East Sussex, and Hants *C. viride* is rare or very rare, locally common in Berkshire, and common in West Sussex. In these same areas all the other species are common or locally common, except for the Bee Orchis, which is rather rare in Hampshire. *H. chlorantha* is decidedly more abundant than *C. viride* but much less so than the other species, although it must be emphasized that these are uncertain in their occurrence and exhibit marked fluctuations in their flowering.

Miss Downie (1941) has recently shown that good germination of *Coeloglossum viride*, *Gymnadenia conopsea* and *Orchis maculata*, can take place, even in distilled water, without any fungal associate. On the other hand *Listera ovata* and *Habenaria bifolia* germinated poorly without the symbiont fungus and only in the presence of organic nutrients.

It may well be that conditions favourable for the development of Orchid seedlings only obtain intermittently and that they must be regarded as species of intermittently available habitats. If this be so their high outputs of seed are probably connected with this rather than with high mortality, but their magnitude compared with that of the Broomrapes is larger, having regard to the much greater risks of failure to reach a suitable locus to which the seeds of the latter are subject.

# XII

# REPRODUCTION IN THE GENUS *HYPERICUM* (ST. JOHN'S WORTS)

The genus *Hypericum*, as represented in the British Flora, comprises some twelve species and reproductive data have been obtained in respect of ten of these. From the point of view here considered the genus is of interest as presenting a rather wide range of soil and habitat conditions. With the exception of *Hypericum undulatum*, which is very restricted in its distribution, all the other British species here considered have a high comital frequency in England, although several are rather local and their abundance sometimes very low. Their frequency and abundance are in fact markedly different.

| Species | Comital frequency in England | Habitat |
|---|---|---|
| Hypericum humifusum | 100 | Heaths on light soils |
| ,, acutum | 99 | Damp places |
| ,, perforatum | 99 | Woodland margin and scrub |
| ,, pulchrum | 99 | Dry heaths |
| ,, androsaemum | 90 | Woodland margins |
| ,, dubium | 90 | Damp places |
| ,, hirsutum | 90 | Woodland margins on calcareous soil |
| ,, elodes | 79 | Peaty pools |
| ,, montanum | 70 | Calcareous rocks and woodland margins |
| ,, undulatum | 7 | Bogs |

This is particularly well exemplified by *H. Androsaemum*, which, though present in 90 per cent of the comital and vice-comital areas in England, is nevertheless relatively rare except in the west, and even there the individuals are usually few in any one spot (*cf.* Salisbury, E. J., 1932, " East Anglian Flora," Map 55). *H. montanum* also, though found in 70 per cent of the comital areas, is a comparatively rare plant throughout. *H. pulchrum* and *H. humifusum*, though both widely distributed, are of decidedly local occurrence.

(1) *Hypericum acutum* Moench. (*tetrapterum* Fries)

The capsules were counted upon thirty-three plants and ranged in number from 13 to one thousand one hundred and forty-eight. The average number of capsules was $160 \pm 23{\cdot}2$, with a standard deviation of 198·3 and a standard error of the mean of 34·8.

The seeds were counted in thirty-six capsules and ranged from 62 to two hundred and seventy-nine. The average number of seeds per capsule was 155 $(154{\cdot}83) \pm 5{\cdot}7$, with a standard deviation ($\sigma$) of 51·79 and a standard error of 86·3. The actual numbers were as follows: 62, 81, 82, 93, 103, 111, 112, 117, 118, 123, 124, 128, 134, 135, 137, 138, 142, 147, 150, 151, 151, 152,

158, 159, 162, 171, 175, 178, 189, 206, 216, 228, 236, 255, 271, 279. In so far as there is an indication of a mode this is evidently between 150 and 160 seeds.

The average seed output based upon these data is therefore 27,962±4,616, or, in round figures, between 23,000 and 32,000 seeds per plant per annum. The average germination in various tests was 66 per cent, giving us an average reproductive capacity of 18,454±3,046.

Thus, the potential offspring of an average plant every year is somewhere between 15,000 and 21,000 seedlings. The largest plant examined would have a potential progeny of over 51,000 per annum.

(2) *Hypericum dubium* Leers.

This species is found in precisely similar habitats to *Hypericum acutum* but is less abundant. It is in general a larger plant with larger flowers and more numerous stamens (*ca.* 20–22 in each of the three groups) than *H. acutum* (*ca.* 8–9 stamens in each of the three groups). It may be that this greater tax upon the food supply which the formation of a flower of *H. dubium* imposes accounts for the fact that in proportion to its larger size as compared with *H. acutum* the flower production is not proportionately greater.

The capsules were counted on 43 plants and ranged in number from twelve to 1,063 capsules per plant. The average number of capsules per plant was 180±22·4, with a standard deviation of 219·3 and a standard error of the mean of 33·7. In a total of thirty-six capsules the number of seeds ranged from 32 to 178, with an average of 75±2·8 ($\sigma$ 25·5; S.E.M. 4·2). The numbers were: 32, 43, 45 (2), 48, 53 (2), 54 (2), 55, 58, 60, 64, 68, 69 (2), 71, 74 (2), 75, 76, 79, 84, 85 (2), 86, 89, 90 (2), 92, 95, 96, 97, 99, 104, 106, 178.

The average seed output on these data is therefore 13,652±2,195, or roughly between 12,000 and 16,000 seeds per plant per annum.

The average germination would appear to be rather low, namely 33 per cent. Germinations as low as 18 per cent have been recorded and the highest germination obtained was 44 per cent. The average reproductive capacity is therefore 4,500±724.

The average seed weight is 0·0000574 gm., giving an average weight per plant of 0·785 gm. of seed; of viable seeds 0·261 gm.

It will be evident from these data that the seed output of *H. dubium* is normally about half that of *H. acutum*, whilst if we can regard the germination tests as giving us a fair estimate of the seedling production in natural conditions the reproductive capacity of *H. dubium* is only about one-quarter of that of *H. acutum*. This may well be an important factor in determining the higher abundance and frequency of *Hypericum acutum*.

(3) *Hypericum undulatum* Schousb. (Plate II)

This species, as we have seen, has a very restricted range in England and is a markedly Oceanic type. It frequents wetter situations than the two preceding species, but from its former inclusion in the aggregate *Hypericum quandrangulum* L. has much in common with them morphologically, although floristically there is an approach to *H. pulchrum*.

The rarity of this species resulted in only eleven specimens being examined. These bore from 15 to 517 capsules, with an average of 149±35·5 capsules per plant ($\sigma$ 175; S.E.M. 53·3).

The seeds were counted in twenty-five capsules and ranged in number from 73 to three hundred and thirty-eight. The average number of seeds was 235±7 ($\sigma$ 52·6; S.E.M. 10·5). The numbers of seeds thus shows a wide range, as follows: 73, 143, 191, 203, 207, 208, 209, 212, 221, 226, 228, 230, 234, 235, 243, 250, 251, 268 (2), 270, 276, 281, 293, 318, 338. The average seed output is then 35,263±9,385.

The average germination is 31 per cent, with an observed range of from 17 per cent to 47 per cent. Thus the mean reproductive capacity would appear to be 10,931±2,909.

The average seed weight is 0·0000378 gm., giving an average weight of seeds per plant per annum of 1·36 gm., of which, however, only 0·42 gm. would appear to be normally efficacious.

Clearly the relatively small number of plants examined of this species precludes our attaching great importance to these data; but it is noteworthy that they indicate a lower reproductive capacity than for the two other and commoner closely related species, both of which, moreover, produce seeds that are about one and a half times as heavy as those of *Hypericum undulatum*. On the basis of the much more restricted environmental conditions that *H. undulatum* demands we should have anticipated that, if reproductive capacity were largely conditioned by the risks of mortality, it would be far superior in this respect to the two congeners mentioned instead of being appreciably inferior. One cannot therefore but infer that here again reproductive capacity appears in a positive rôle in relation to frequency and abundance.

(4) *Hypericum pulchrum* L.

This species of dry non-calcareous heaths affords an interesting comparison with the much less common *Hypericum montanum*, which is typically a species of dry calcareous situations. Both may occur as marginal woodland species, and on rocks, the one on calcareous the other on non-calcareous.

Eighty-four plants of *Hypericum pulchrum* were examined, of which the one bearing the smallest number of capsules, namely 2, was a plant growing on a ledge of the non-calcareous rocks in North Wales. The other extreme was represented by a specimen on a peaty heath which bore 649 capsules. The average number of capsules per plant was 71 (70·66)±6 ($\sigma$ 82·8; S.E.M. 9·0).

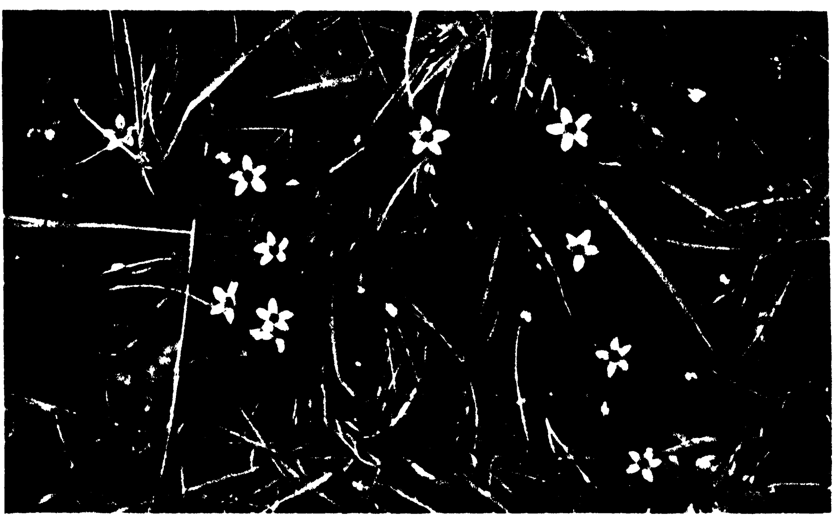
The seeds were counted in fifty-eight capsules and the number of apparently good seeds ranged from 21 to 110. The average number was 63 (62·8)±2·0 ($\sigma$ 23·2; S.E.M. 3). The numbers of seeds were as follows: 21, 24, 27, 29, 32, 35, 37, 38, 39, 40, 43, 44, 45, 46, 47, 49, 50 (2), 51, 52 (2), 53 (3), 54, 55 (2), 56 (2), 58, 59 (2), 61, 64, 65, 73 (2), 75, 77, 78 (2), 81 (2), 82, 85, 87, 90, 92, 93 (2), 96, 105, 106 (2), 107, 110, From which it would appear that the mode may be somewhat lower than the average.

The average seed output was thus 4,449±518, or approximately between 4,000 and 5,000 seeds per plant per annum.

The germination tests showed a viability range of from 78 to 90 per cent,

PLATE II

*Hypericum undulatum*, a rare "Oceanic" species of St. John's Wort which grows in marshes.



*Hypericum humifusum*, a prostrate St. John's Wort of dry heaths.

with a mean value of 83 per cent. Thus, the average reproductive capacity is 3,692±430.

The average weight of a seed is 0·00009 gm., giving an average seed weight per plant per annum of 0·4 gm. and a weight of viable seeds of 0·332 gm.

(5) *Hypericum montanum* L.

Only nine plants of this species were available. These bore from 56 to 474 capsules, with an average of 219±28 capsules per plant (σ 26 ; S.E.M. 42).

The seed contents were examined in thirty capsules, and the seeds ranged in number from 33 to 268 per capsule, as follows: 33, 39, 43, 46, 49, 54, 61, 71, 75, 79, 84, 85, 87, 88, 91, 99, 107, 121, 139, 149, 154, 171, 179, 181, 184, 188, 211, 217, 237, 268. The average number of seeds was 120 (119·66)±7·8 (σ 64·4; S.E.M. 11·7).

The average seed output was therefore 26,424±5,159, or approximately between 21,000 and 31,000 seeds per plant per annum.

The percentage germination of *H. montanum* seeds ranged from 55 to 97 per cent, with an average of 78 per cent, so that the average reproductive capacity is 20,610±4,024.

The average weight of the seed is 0·000053 gm., so that the average weight of seeds per plant per annum is 1·3276 gm. and 1·035 gm. viable seeds.

Of the two species *H. montanum* and *H. pulchrum* the less common has here about five times the reproductive capacity of the more abundant. But it should be noted that the seeds of *H. pulchrum* are heavier than those of *H. montanum*. Even so, the weight of viable seeds per plant of *H. pulchrum* is much less than for *H. montanum*. There is, however, one important difference between the two species with respect to propagation, which, from comparison with other instances, we might expect completely to outweigh the differences in seed production. *H. pulchrum* normally spreads vegetatively by the production of adventitious shoots from its roots (*cf.* Fig. 31) in the same manner as, though less profusely than, *H. perforatum*. As a consequence of this vegetative propagation not only does *H. pulchrum* spread, even in relatively dense herbage which it could not colonize from seed, but the individual attains a sort of potential immortality, since though the oldest parts eventually die the vigour is perpetually maintained by means of these vegetative progeny. *H. montanum*, on the other hand, does not reproduce in this way, and from my own experience of this species when grown in a garden it would appear to be a comparatively short-lived perennial, though it is possible that under wild conditions it may be of longer duration.

(6) (Hairy St. John's Wort) *Hypericum hirsutum* L.

From an examination of fifty-one plants, all apparently adult, the average number of fruits per plant was found to be 356 (355·9)±23·8, with a range from 36 to 1,215 fruits (σ 253·5; S.E.M. 35·7).

The seeds were counted in thirty-six capsules, as follows: 36 (2), 39, 42 (2), 51, 53, 55, 57, 61, 62, 64, 65, 66 (2), 67, 69, 72 (2), 78, 80, 81 (2), 82, 84, 85, 87, 91, 92, 96, 98 (2), 107 (2), 116. The number ranged from 36 to 116 seeds, with an average of 72·3±2·28 (σ 20·57; S.E.M. 3·43).

The average seed output is therefore 25,789±2,535 seeds per plant per annum, or approximately between 23,000 and 28,000 seeds.

The average germination is 70 per cent, with an observed range of from 12 to 88 per cent. Thus, the average reproductive capacity is about 18,000±1,774 offspring per plant per annum.

The mean seed weight is 0·0000905 gm., or an average weight of seeds per plant of 2·334 gm. and 1·62 gm. per plant per annum of viable seeds.

*Hypericum hirsutum* has similar soil preferences to *H. montanum*, and, like that species, does not exhibit any special mode of vegetative propagation. Their reproductive capacities are very similar, with an apparent balance in favour of *H. montanum*, though in view of the small number of individuals of the latter species no significance can be attached to this difference. It is, however, important to note that the seeds of *H. montanum* are appreciably lighter than those of *H. hirsutum*, so that the annual average weight of viable seeds is over one and a half times as great for *H. hirsutum* as for *H. montanum*.

(7) (Perforate St. John's Wort) *Hypericum perforatum* L.

This is alike the most widespread of the British *Hypericums* and the most abundant in individuals. Forty-four plants were examined for capsule numbers, and these ranged from 67 to 1,823 per plant. The total number of capsules counted on the 44 plants was 15,800, or an average of 359±32·2 ($\sigma$ 319·8; S.E.M. 48·4).

In twenty-five capsules the number of seeds ranged from 43 to 127, with an average of 84 (84·1)±2·8 seeds per capsule ($\sigma$ 21·0; S.E.M. 4·2), as follows: 43, 50, 53, 56, 67, 70, 73, 76 (2), 79, 80, 81 (2), 83, 88, 90 (2), 93, 101, 102 (2), 104, 118, 119, 127.

The average seed output from these data would therefore be 30,282±3,713, or approximately between 26,000 and 34,000 seeds per plant per annum.

The average germination is 43 per cent, with an observed range of from 15 to 54 per cent. Thus, the reproductive capacity is approximately 13,000±1,596 potential offspring per plant per annum.

It must, however, be borne in mind that *Hypericum perforatum* reproduces very freely by vegetative means. From even the finest of the more superficial horizontal roots adventitious shoots may be produced, and removal of the aerial shoots by browsing, or any other check to their growth, usually results in profuse propagation by this means which enables the species to extend in relatively dense vegetation, although seedlings are usually restricted to better illuminated areas. It is undoubtedly this vegetative propagation rather than the propagation by seeds that accounts for the abundance of the species. Though, however, the reproductive capacity is lower than some of the other species it should be noted that the seeds are the heaviest of any of the British terrestrial species, namely 0·0001 gm. The annual average weight of viable seeds per plant is therefore 1·3 gm., a figure only exceeded by that for *H. hirsutum*, in which there is no such vegetative mode of propagation.

(8) *Hypericum humifusum* L. (Plate II)

Two features of this species would lead one to anticipate a high reproductive

capacity if the main determining factor in the rate of reproduction be the risks of mortality. These features are firstly the short-lived character of the plant, which, though classed as a perennial in the floras, is not infrequently monocarpic, and in my own experience with a considerable number of plants its duration is rarely more than 2 or 3 years. Secondly, unlike its congeners, it is prostrate in habit, so that the chances of dispersal of the seeds are far less than for the erect species, and competition amongst the offspring is liable to be much more severe.

On sixty-five plants the number of capsules ranged from 4 to 395, with an average of 69 (68·84)$\pm$5·1 ($\sigma$ 61·2; S.E.M. 7·65).

The seeds in 38 capsules numbered 3,741, giving an average of 98·9 seeds per capsule $\pm$4·1 ($\sigma$ 37·5; S.E.M. 6·2), as follows: 24, 40, 42, 50, 51, 58, 63, 65, 66, 73, 74, 77 (2), 80, 81 (2), 83, 84, 94, 97, 104, 108, 110, 113, 114, 116, 122, 126, 130 (3), 145, 146 (2), 149, 152, 161, 181. The range was from 24 to 181 seeds per capsule.

The average seed output is therefore 6,829$\pm$787, or approximately between six thousand and seven thousand six hundred seeds per plant.

The average germination is 61 per cent, so that the average reproductive capacity is 4,165$\pm$480 potential offspring per plant.

The average weight of a seed is 0·0002 gm., which is the lightest of all the seeds of the species here dealt with. The average weight of viable seeds per plant is therefore 0·0833 gm. It is scarcely surprising, therefore, that this species is associated with open vegetation, and though found in all the comital and vice-comital areas of England is nevertheless decidedly local in its occurrence.

### (9) Tutsan, *Hypericum androsaemum* L.

The chief interest of this species is that it is a shrubby member of the marginal flora of woodlands on light soils, but, for its habitat, has comparatively light seeds, viz. 0·0000625 gm.

The capsules were counted on twenty-six plants, and ranged in number from 22 to three hundred and one. The average number was 117$\pm$10·6 per plant per annum ($\sigma$ 80·1; S.E.M. 16).

The seeds per capsule are very numerous, ranging from 529 to 1,079 in the fifteen capsules in which they were counted, as follows: 529, 605, 707, 712, 804, 862, 865, 902, 927, 961, 984, 1,049, 1,061, 1,062, 1,079. The average number was 874$\pm$29·2 ($\sigma$ 166·7; S.E.M. 43·8).

The average seed output is thus 102,567$\pm$12,681, or approximately between 90,000 and 115,000 seeds per plant per annum.

The average germination is 78 per cent, with an observed range of from 61 to 96 per cent. The average reproductive capacity is thus 80,000$\pm$9,891 potential offspring per plant per annum. The average weight of viable seeds per plant is thus 5·0 gm.

### (10) *Hypericum elodes*

This, the sole British aquatic species of the genus, spreads vegetatively in the peaty silt which it frequents, rooting repeatedly at the nodes, so that it is impossible to distinguish separate individuals except when very young. For

this reason no attempt was made to estimate the number of seeds produced per plant.

The number of capsules which are produced per inflorescence is small in comparison with other species. They normally range from three to nine, with an average of $5 \pm 0 \cdot 3$ capsules ($\sigma$ 1·93; S.E.M. 0·45). The seeds were counted in fifty-eight capsules, and ranged in number from 6 to 75, with an average of 42 (41·8)$\pm$1·36 seeds per capsule ($\sigma$ 15·5; S.E.M. 2·04). The numbers were as follows: 6, 8, 9, 16, 21 (2), 22, 23 (3), 24, 26, 29, 31 (3), 33 (2), 34, 35, 36, 37 (2), 41 (2), 43 (2), 44, 45, 46 (3), 47, 48 (2), 50 (5), 51, 52, 53, 54, 55 (3), 56 (3), 57, 58, 60, 61 (2), 66, 69, 75. From which it is seen that over 29 per cent of the capsules contain between fifty and sixty seeds. Thus the average number of seeds per inflorescence is $209 \pm 19$.

It would only be possible to compare with other species on a basis of unit area, from which it is almost certain that the seed output would be found to be low for *Hypericum elodes*.

Few germination tests are available, but it is probable that the average germination is under 5 per cent. It will therefore be evident that the reproductive capacity by means of seeds is very low, although vegetative propagation is high. It is in conformity with these facts that *H. elodes* is often extremely abundant over considerable areas in suitable habitats but is not infrequently absent from isolated ponds, etc., where its presence might have been expected.

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The species of *Hypericum* can then be said to support the view that reproductive capacity is a positive asset to the species, and that for species having no special means of vegetative spread the higher the potential reproductive capacity of the species the commoner the species tends to be. On the other hand, the importance of vegetative spread is manifest, and it is noteworthy that, of all the species, that in which vegetative propagation is most marked, namely *H. perforatum*, is by far the commonest. Of the square-stemmed species it should be remarked that all exhibit vegetative propagation to a limited extent, but more so in *H. acutum* and *H. dubium* than in *H. undulatum*. *Hypericum pulchrum*, as already noted, spreads vegetatively, and, contrary to published statements, by means of adventitious shoots which arise from the roots (*cf.* Fig. 31).

The species of *Hypericum* also afford evidence that the average reproductive weight may have some significance in determining frequency and abundance.

# XIII

# REPRODUCTION IN THE GENTIANACEAE

The Gentianaceae are of especial interest from two aspects. Firstly, they present a series of species which are characterized by seeds of rather diverse weights though mostly very light. Secondly, they are mycorrhizal plants, and the great difficulty of cultivating some species and the almost impossible task of growing others for more than a year or two (*e.g. Gentiana bavarica*, which I understand cannot be grown for any length of time in gardens, even in Switzerland) has been attributed to this fact. We may presume that the mycorrhizal relation is an obligate one, and it is probable that the minute amount of food reserve is for this reason not an undue handicap. Some members of the group, however, are easily grown, and this is particularly true of *Menyanthes trifoliata*, which is apparently devoid of mycorrhizal infection. The group probably therefore includes a range with respect to the method of nutrition from those, like *Menyanthes* and *Villarsia*, apparently devoid of mycorrhiza and completely dependent upon their own photosynthesis and metabolism through various degrees of mycorrhizal relationship to the completely saprophytic types belonging to the genera *Voyria* and *Voyriella*. Nevertheless, it is characteristic of a considerable number of gentianaceous plants that they are found in open situations. Thus, *Chlora perfoliata*, *Erythraea* spp., *Gentiana anglica*, *Gentiana nivalis*, *Cicendia filiformis*, and many others, are species either of bare ground or very short and open turf.

Yellow Centaury, *Chlora perfoliata* L. (Blackstonia)

This species of the chalk is an annual or biennial, whose seedlings are often met with on almost bare soil but can colonize in well-browsed pasture. The situations it frequents are commonly very well drained, as, for example, the slopes of the chalk downs or the more calcareous types of dunes. It is, however, sometimes encountered in dune slacks where the water content is high but the soil solution rich in bases. In the drier stations, which are more typical, the plants are not infrequently depauperate, so that it is scarcely surprising to find that small plants are those having the highest frequencies.

The capsules were counted on 180 plants, and, as shown in Table XXXIX, exhibited a range of from one to 294 capsules per plant. The average is 13·4 capsules per plant ($\pm 1{\cdot}28$), but it should be noted that the majority of the population (54·4 per cent) bear from 2–9 capsules only. The standard deviation is 25·8 and the standard error of the mean 1·92.

The seeds were counted in twenty capsules and totalled 13,696, or an average of 685 (684·8)$\pm$32·1 seeds per capsule ($\sigma$ 215·6; S.E.M. 48·2). The actual numbers of seeds in the capsules examined, in descending order, was as follows: 1,179, 1,046, 956, 859, 780, 752, 734, 719, 705, 697, 643, 630, 626, 613, 603, 565, 545, 439, 434, 171. Although the number of capsules examined was small the standard error of the mean is not large, and, moreover, the

TABLE XXXIX. VARIATION IN CAPSULE NUMBER IN *CHLORA PERFOLIATA* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 5 | 11 | 9 | 22 | 2 | 45 | 1 |
| 2 | 12 | 12 | 5 | 23 | 3 | 46 | 1 |
| 3 | 15 | 13 | 3 | 24 | 3 | 47 | 1 |
| 4 | 9 | 14 | 7 | 25 | 4 | 54 | 1 |
| 5 | 12 | 15 | 1 | 27 | 2 | 55 | 1 |
| 6 | 13 | 16 | 4 | 28 | 3 | 60 | 1 |
| 7 | 13 | 17 | 3 | 29 | 2 | 294 | 1[1] |
| 8 | 8 | 18 | 6 | 30 | 1 | | |
| 9 | 16 | 19 | 3 | 41 | 1 | | |
| 10 | 6 | 20 | 1 | 43 | 1 | | |

[1] This exceptionally large plant was found on Braunton Dunes.

fact that the average number of seeds is a figure which lies between the ten higher and the ten lower numbers of seeds suggests a greater accuracy than might have been expected from the high number of seeds concerned and the wide range of variation.

The average seed output on these data is therefore 9,219$\pm$1,305 seeds per plant. Germination in nature normally takes place in autumn, and although no exact figures are available the germination of freshly harvested seed on calcareous soils is usually high.

The average weight of the seeds is 0·0000107 gm., so that the average weight of seeds produced by a single plant is about 0·1 gm.

Having regard to the average size of a plant it will be realized that the seed output is very high. The average number of capsules is lower than it otherwise would be, through the high proportion of relatively depauperate individuals, but attention may be called to the large size which isolated individuals can attain, as shown by the specimen which bore 294 capsules. Such an individual would produce more than 200,000 seeds: a seed production which probably surpasses that of most parasites of comparable size. A very striking feature of this species is that it may occur on an area in large numbers but in the following years is often only sparsely represented, thus suggesting an intermittency of favourable habitat conditions.

*Cicendia filiformis* Delarb.

One hundred and ten plants of this species were examined. The numbers of capsules they bore are given below:

TABLE XL. VARIATION IN NUMBER OF CAPSULES ON *CICENDIA FILIFORMIS*

| Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|
| 1 | 54 | 6 | 1 |
| 2 | 33 | 7 | – |
| 3 | 9 | 8 | – |
| 4 | 7 | 9 | 1 |
| 5 | 5 | | |

Total 215 capsules, 110 plants.

The average number of capsules per plant was 1·95±0·09 (σ 1·35; S.E.M. 0·13). The seeds were counted in seven capsules, and ranged in number from 70 to one hundred and eighty-six. The average number was 149±10·6 (σ 41·3; S.E.M. 15·9).

Thus the average seed production would be 291±34 seeds per plant; a remarkably high number having regard to the small size of even the largest individuals and the very restricted photosynthetic surface that *Cicendia filiformis* presents. Of this species, too, the population exhibits striking fluctuations in numbers.

Pink Centaury, *Erythraea Centaurium* Pers.

This species, though characteristically a plant of dry soils, especially chalk downs and calcareous dunes, is also a feature of coppiced areas and other clearings in woodlands. It is thus a plant of open habitats but has much heavier seeds than *Chlora perfoliata*. The average weight of a seed of *Erythraea Centaurium* is 0·000026 gm., or about two and a half times that of *Chlora*.

One hundred and seventy-three specimens of *E. Centaurium* were examined for fruit production, and the data for these are furnished in Table XLI, from which it will be seen that the number of capsules per plant ranged from 4 to four hundred and eighteen. The average number was 43·4±2·8 (σ 55·5; S.E.M. 4·2); but here again the mode is much lower than the mean.

TABLE XLI. PINK CENTAURY, *ERYTHRAEA CENTAURIUM*. VARIATION IN NUMBER OF CAPSULES PER PLANT

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 4 | 3 | 23 | 5 | 42 | 2 | 86 | 1 |
| 5 | 0 | 24 | 3 | 43 | 1 | 87 | 1 |
| 6 | 3 | 25 | 4 | 44 | 2 | 88 | 1 |
| 7 | 1 | 26 | 2 | 45 | 3 | 89 | 2 |
| 8 | 1 | 27 | 5 | 46 | 1 | 96 | 1 |
| 9 | 3 | 28 | 1 | 47 | 1 | 98 | 1 |
| 10 | 3 | 29 | 3 | 48 | 1 | 100 | 2 |
| 11 | 8 | 30 | 3 | 49 | 3 | 102 | 1 |
| 12 | 5 | 31 | 3 | 50 | 2 | 115 | 1 |
| 13 | 4 | 32 | 3 | 55 | 2 | 122 | 1 |
| 14 | 5 | 33 | 3 | 60 | 1 | 139 | 1 |
| 15 | 4 | 34 | 4 | 65 | 1 | 157 | 2 |
| 16 | 1 | 35 | 3 | 66 | 1 | 244 | 1 |
| 17 | 8 | 36 | 3 | 75 | 1 | 278 | 1 |
| 18 | 7 | 37 | 1 | 77 | 1 | 312 | 1 |
| 19 | 6 | 38 | 1 | 78 | 2 | 326 | 1 |
| 20 | 6 | 39 | 1 | 79 | 2 | 418 | 1 |
| 21 | 2 | 40 | 1 | 81 | 2 | | |
| 22 | 3 | 41 | 1 | 83 | 1 | | |

The seeds were counted in twelve ripe but undehisced capsules, their number ranging from 75 to 334, with an average of 249 (248·6)±11·9 (σ 62·7; S.E.M. 17·9). From which the average number of seeds per plant would be 10,840

$\pm$1,214, or approximately between 10,000 and 12,000 seeds. This represents an average weight of seeds per plant of about 0·28 gm.

### Gentiana Species

The species of this genus occupy a wide range of habitats. Some, like *G. nivalis*, occupy bare places on rocks; others, like *G. campestris* L. and *G. anglica* Pugsley, comparatively open places in short turf. *G. pneumonanthe* grows in fairly dense vegetation in marshes, whilst amongst exotics *G. lutea* is typically a meadow species and *G. asclepidea* a plant of subalpine woodlands. The various species show an appreciable range in seed weight and fall roughly into two classes: those with minute seeds less than one-tenth of a milligram in weight, and those with seeds exceeding one-tenth of a milligram. To the former class belong *G. nivalis* (0·000015 gm. to 0·000037 gm.), *G. verna* (0·000033 gm.) and also the marsh species *G. pneumonanthe* (0·000025 gm.). To the second class belong the members of the *amarella* group, species of open short turf communities, and well exemplified by *G. lingulata v. praecox* (0·000128 gm.), also the woodland *G. asclepidea* (0·000132 gm.), and *G. purpurea*, a characteristic species of the alpine meadows, with seeds which, according to Vogler, weigh 0·00046 gm. It will be evident from these data that, although from their mycorrhizal habit the members of this genus may be far less dependent than non-mycorrhizal plants upon the reserve of food in the seed, the species of Gentiana which are features of the denser types of plant community would appear to possess the heavier types of seed.

#### Felwort, *Gentiana axillaris* Reichb. (*G. amarella*)

A total of 214 plants of this species from Buckinghamshire, Hertfordshire and Sussex were examined for the number of fruits produced. These ranged from one to sixty-two, as shown in the accompanying Table XLII. The average number of capsules was 17·24$\pm$0·49 ($\sigma$ 10·79; S.E.M. 0·73), whilst there is a mode between eight and thirteen.

TABLE XLII. VARIATION IN NUMBER OF FRUITS OF *GENTIANA AXILLARIS*

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 14 | 9 | 27 | 2 | 40 | 2 |
| 2 | 0 | 15 | 7 | 28 | 2 | 41 | 0 |
| 3 | 2 | 16 | 10 | 29 | 2 | 42 | 1 |
| 4 | 3 | 17 | 5 | 30 | 2 | 43 | 2 |
| 5 | 3 | 18 | 8 | 31 | 2 | 44 | 1 |
| 6 | 2 | 19 | 8 | 32 | 4 | 48 | 1 |
| 7 | 9 | 20 | 5 | 33 | 1 | 49 | 1 |
| 8 | 11 | 21 | 6 | 34 | 1 | 53 | 2 |
| 9 | 19 | 22 | 5 | 35 | 1 | 54 | 1 |
| 10 | 15 | 23 | 1 | 36 | 1 | 58 | 1 |
| 11 | 16 | 24 | 2 | 37 | 1 | 62 | 1 |
| 12 | 11 | 25 | 2 | 38 | 1 | | |
| 13 | 13 | 26 | 8 | 39 | 0 | | |

Total of 3,691 capsules on 214 plants.

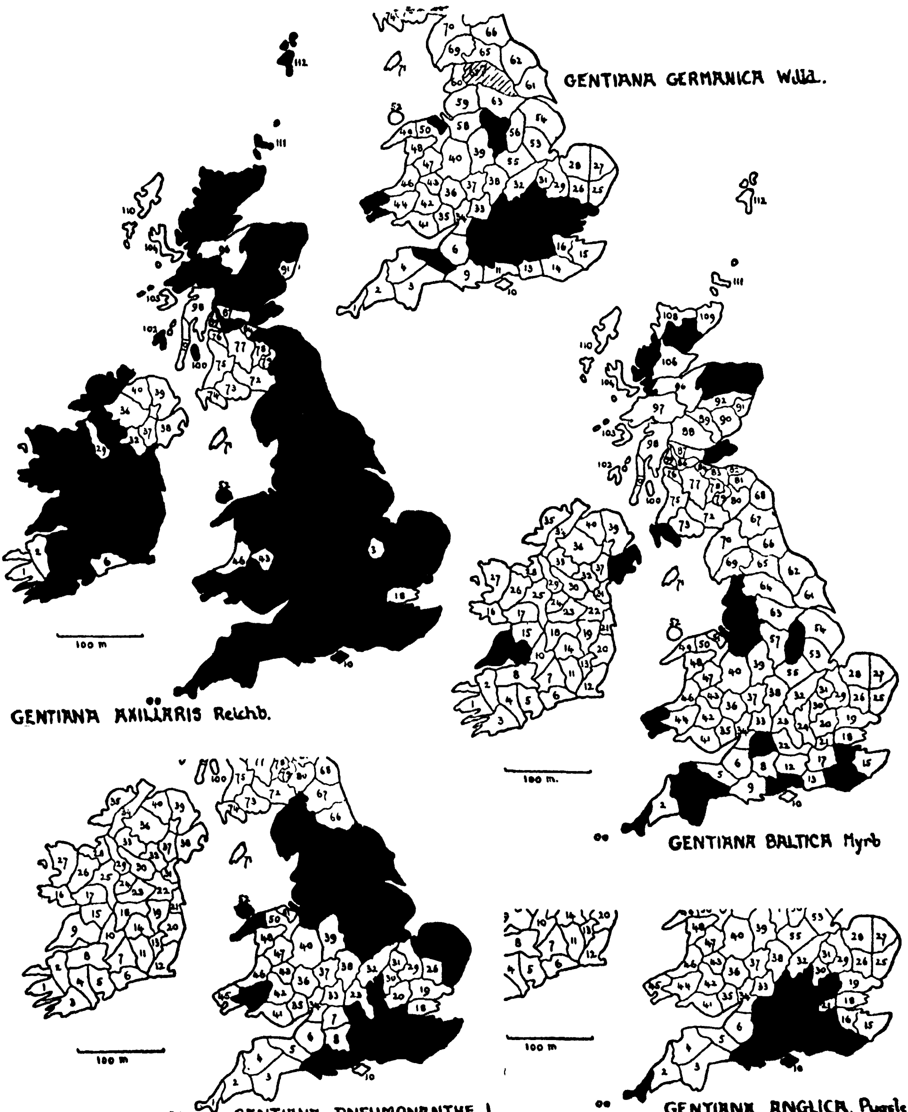


FIG. 22. Maps showing the distribution in the British Isles of five species of Gentian. The counties in which the species has been found are shown in black, even though it may have been recorded from but a single station. The Felwort (*Gentiana axillaris*) is the most widespread and the most abundant. *G. baltica* is widely distributed but much more local. The Marsh Gentian (*G. pneumonanthe*), *Gentiana germanica*, and the Summer Gentian (*G. anglica*), show, in the order named, an increasing restriction towards the south.

35 (1), 39 (2), 41 (2), 44 (1), 46 (1), 48 (1), 49 (1), 50 (1), 52 (1), 54 (1), 56 (1), 57 (1), 58 (1), 60 (2), 61 (1), 62 (1), 65 (1), 69 (1), 70 (1), 74 (1), 76 (2), 77 (1), 79 (2), 82 (1), 85 (1), 91 (1).

The average seed output per plant is thus 325±23 seeds.

Marsh Gentian, *Gentiana Pneumonanthe* L.

All the species hitherto considered are annuals, or at most monocarpic biennials, but the present species of marshy habitats is a perennial, probably of appreciable duration, though the very striking fluctuations in number of inflorescences of *G. Pneumonanthe* in different seasons may represent a fluctuation of population and not merely of flowering specimens.

One hundred and eighty-one plants of *G. Pneumonanthe* were examined for fruit production for which the data are furnished below:

TABLE XLVI. VARIATION IN NUMBER OF FRUITS PER PLANT OF *GENTIANA PNEUMONANTHE* L.

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|
| 1 | 59 | 7 | 3 |
| 2 | 37 | 8 | 0 |
| 3 | 43 | 9 | 2 |
| 4 | 17 | 10 | 1 |
| 5 | 14 | 11 | 0 |
| 6 | 4 | 12 | 1 |

Total of 485 capsules on 181 plants.

The average number of capsules is 2·68 per plant (±0·05 $\sigma$ 1·1; S.E.M. 0·08), whilst the mode is a single fruit.

Only three capsules have been examined for seed numbers, and these contained respectively 433, 405, and 491 seeds, an average of 443±13·3. The seed output per plant would therefore appear to be about 1,188±89 seeds per annum, a far larger seed production than that of any of the monocarpic types considered.

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If we place the species of Gentian here considered in the order of their average seed outputs the sequence is as follows:

| | Average seed output | Comital and vice-comital frequency in England (percentage) |
|---|---|---|
| Gentiana anglica Pugsley | 295 | 19·7 |
| ,, baltica Myrb. | 325 | 18·0 |
| ,, germanica Willd. | 623 | 22·5 |
| ,, axillaris Reichb. | 862 | 94·4 |
| ,, Pneumonanthe L. | 1,188 | 43·6 |

It will be evident that so far as the monocarpic species are concerned the order of increasing seed output corresponds approximately with that of

increasing frequency in England (*cf.* Fig. 22). Since *G. baltica* is found in Scotland as well as England, whereas *G. anglica* does not occur north of the line extending from the Bristol Channel to the Wash, it is reasonable to assume that the former is the hardier type, especially as the latter is a " winter annual," and thus the probabilities are in favour of a higher seedling mortality for *G. anglica* than for *G. baltica;* yet the seed output of the hardier species is the greater. *G. Pneumonanthe* has not only the largest seed output but is also perennial; its potential replacement capacity thus far exceeds that of the annual and biennial species. Its very light seeds provide little food reserve for the seedling but ensure adequate dispersal, and there can be no doubt that the comparative infrequency of this species is due to the specialized edaphic conditions which it demands. In the absence of adequate germination data for the different species it must suffice to state that *G. Pneumonanthe* would appear to be at least as easy to germinate as the other species if suitable conditions are provided, but it may well be that such conditions are for this species far more intermittent in their incidence.

# XIV

# THE GENUS *LINARIA* (TOADFLAX)

The British members of this genus afford us comparison between perennial and annual species, and the latter comprise the erect *L. minor* and the prostrate *L. elatine* and *L. spuria*. All of the three annual species germinate in the late spring or early summer.

## Little Toadflax, *Linaria minor* Desf.

This species in nature normally germinates in the late spring, about the end of April or beginning of May, though Brenchley and Warrington found that buried seeds of this species germinated in an unheated greenhouse mainly between January and March.

One hundred and forty-nine plants were examined for fruit production, the data for which are furnished in Table XLVII.

TABLE XLVII. VARIATION IN CAPSULE PRODUCTION OF *LINARIA MINOR* DESF.

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 15 | 2 | 29 | 0 | 80 | 2 |
| 2 | 4 | 16 | 4 | 30 | 1 | 82 | 1 |
| 3 | 1 | 17 | 1 | 35 | 2 | 104 | 1 |
| 4 | 5 | 18 | 1 | 36 | 1 | 106 | 1 |
| 5 | 19 | 19 | 3 | 39 | 2 | 120 | 1 |
| 6 | 9 | 20 | 0 | 42 | 1 | 126 | 1 |
| 7 | 14 | 21 | 1 | 43 | 1 | 137 | 1 |
| 8 | 8 | 22 | 2 | 44 | 1 | 188 | 1 |
| 9 | 16 | 23 | 0 | 47 | 1 | 250 | 1 |
| 10 | 7 | 24 | 2 | 52 | 1 | 263 | 1 |
| 11 | 6 | 25 | 2 | 58 | 1 | 320 | 1 |
| 12 | 2 | 26 | 0 | 70 | 1 | 363 | 1 |
| 13 | 5 | 27 | 2 | 73 | 1 | 476 | 1 |
| 14 | 1 | 28 | 0 | 74 | 1 | | |

Total of 4,661 capsules on 149 plants.

The average number of fruits per plant is therefore $31{\cdot}3 \pm 3{\cdot}5$ ($\sigma$ 65; S.E.M. 5·3).

Sixteen capsules were examined for seed number, which ranged from 40 to one hundred and three. The average number of seeds per capsule was $69 \pm 2{\cdot}5$ ($\sigma$ 15·4; S.E.M. 3·8). Thus the average seed output is $2{,}168 \pm 320$ per plant. The average weight of a seed is 0·000067 gm., so that the average weight of seed per plant is approximately 0·145 gm. Owing to its erect habit and the smaller size and weight of the seeds *Linaria minor* has a much more efficient seed dispersal than the two prostrate annual species, the seeds of which probably depend for their dispersal mainly upon rainwash.

Fluellen, *Linaria spuria* Mill.

The size of the plants of this species and of *L. Elatine* show a wide range; for whilst the majority of the individuals are relatively small there are also occasional individuals of exceptionally large size. Thus the range in number of fruits borne by the plants examined was from 4 to two thousand and forty-seven. The distribution is shown in Table XLVIII.

TABLE XLVIII. *LINARIA SPURIA* MILL. VARIATION IN NUMBER OF FRUITS PER PLANT

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 4 | 1 | 30 | 1 | 51 | 1 | 101 | 1 |
| 5 | 3 | 31 | 2 | 54 | 1 | 105 | 2 |
| 8 | 1 | 33 | 1 | 57 | 1 | 106 | 1 |
| 11 | 1 | 34 | 1 | 58 | 1 | 111 | 1 |
| 13 | 1 | 35 | 2 | 63 | 2 | 115 | 1 |
| 14 | 2 | 36 | 1 | 64 | 2 | 154 | 1 |
| 17 | 1 | 38 | 1 | 65 | 1 | 174 | 1 |
| 18 | 1 | 39 | 1 | 68 | 1 | 185 | 1 |
| 19 | 3 | 40 | 1 | 69 | 1 | 206 | 1 |
| 21 | 1 | 41 | 3 | 70 | 1 | 217 | 1 |
| 22 | 1 | 42 | 2 | 72 | 1 | 241 | 1 |
| 23 | 1 | 43 | 1 | 73 | 1 | 268 | 1 |
| 24 | 1 | 44 | 1 | 76 | 1 | 315 | 1 |
| 25 | 1 | 45 | 1 | 79 | 1 | 330 | 1 |
| 27 | 1 | 47 | 1 | 80 | 1 | 2,047 | 1 |
| 28 | 1 | 48 | 1 | 86 | 1 | | |
| 29 | 3 | 49 | 1 | 88 | 2 | | |

Total of 7,503 capsules on 82 plants.

The average number of capsules is $91{\cdot}5 \pm 16{\cdot}8$ ($\sigma$ 227; S.E.M. 25·2). It may be emphasized that the specimens examined represent all those present in their several localities and may therefore perhaps be regarded as a random sampling of the population of this species. But inasmuch as *L. spuria* is a "summer annual," whose seeds in natural conditions normally germinate towards the end of May, or even later, it is evident that the size attained by the individuals will be liable to considerable variation as between different seasons according to the character of the summer weather. Further, as I have elsewhere pointed out (1939, *Quart. Jour. Roy. Met. Soc.*, LXV, p. 343), the effective fruiting of this species is markedly influenced by the autumn temperatures and incidence of early frosts. In this connection the observations of Michalet (1860, p. 468) should be noted, that *Linaria spuria* can produce cleistogamic flowers, since such may develop under conditions of lower light intensity and temperature than is requisite for normal flower formation.

The number of seeds was investigated in 159 capsules, taken from four plants of different sizes, bearing respectively 63 capsules, 206 capsules, 315 capsules, and 2,047 capsules. The data are given in Table XLIX.

It will be at once evident that the means are very similar, despite the great diversity in size of the parent plants, and they bear out the conclusion already

TABLE XLIX. VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *LINARIA SPURIA* Mill.

| Seeds per capsule | Number of capsules on plant bearing 63 capsules | 206 capsules | 315 capsules | 2,047 capsules |
|---|---|---|---|---|
| 10 | 0 | 0 | 0 | 1 |
| 11 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 0 | 2 |
| 13 | 0 | 0 | 0 | 1 |
| 14 | 0 | 0 | 1 | 0 |
| 15 | 0 | 0 | 1 | 0 |
| 16 | 1 | 0 | 0 | 0 |
| 17 | 1 | 0 | 1 | 1 |
| 18 | 0 | 1 | 4 | 1 |
| 19 | 0 | 0 | 1 | 8 |
| 20 | 2 | 0 | 2 | 1 |
| 21 | 1 | 1 | 2 | 4 |
| 22 | 0 | 2 | 4 | 8 |
| 23 | 1 | 0 | 1 | 5 |
| 24 | 2 | 0 | 5 | 4 |
| 25 | 2 | 1 | 5 | 1 |
| 26 | 1 | 1 | 1 | 5 |
| 27 | 3 | 0 | 4 | 8 |
| 28 | 2 | 1 | 6 | 5 |
| 29 | 2 | 2 | 3 | 3 |
| 30 | 1 | 0 | 1 | 5 |
| 31 | 3 | 0 | 2 | 4 |
| 32 | 2 | 0 | 4 | 4 |
| 33 | 0 | 0 | 0 | 1 |
| 34 | 0 | 0 | 1 | 0 |
| 35 | 1 | 0 | 0 | 2 |
| 36 | 0 | 0 | 0 | 0 |
| 37 | 0 | 0 | 1 | 0 |
| 38 | 0 | 0 | 0 | 1 |
| Totals | 25 | 9 | 50 | 75 |
| Means | 26·3 | 24·4 | 25·1 | 24·55 |
| | $\sigma$ 4·77 | $\sigma$ 3·68 | $\sigma$ 5·06 | $\sigma$ 5·54 |
| S.E.M. | 0·95 | 1·22 | 0·72 | 0·64 |

arrived at from the study of other species that the number of seeds in the fruit is not appreciably affected by the size of the individual bearing them. The difference between the means for the smallest and largest plants is 1·75, but the standard error of this difference is 1·14, so that it is clearly not "significant." Actually the mean number of seeds is highest for the individual bearing only sixty-three capsules, a feature which may well be associated with the prolonged fruiting period of the plant, as an outcome of which there is apt to be a diminution in size of the capsules as the season progresses. So the proportion of large capsules tends to be greater the smaller the number produced.

The average number of seeds for all the 159 capsules is 25 (24·9)$\pm$0·27 ($\sigma$ 5·22; S.E.M. 0·41). The average seed output is therefore 2,282$\pm$443 seeds per plant.

The germination would appear to be low. In several tests the highest percentage obtained was 12 per cent, but the viability of seeds in this country probably varies appreciably with the climatic conditions in late autumn.

The average seed weight is 0·000394 gm., so that the average weight of seed per plant would be about 0·77 gm.

Fluellen *Linaria Elatine* Mill.

A total of eighty-three plants was examined for fruit production, and showed similar features to the species just considered. The observed range was from 5 to 1,274 capsules per plant, with a mean of 102±12·5 ($\sigma$ 170; S.E.M. 18·8). The data are given in Table L. From this it will be obvious that there is a wide range with a high proportion of relatively small specimens and a few very large ones.

TABLE L. VARIATION IN FRUIT PRODUCTION OF *LINARIA ELATINE* MILL.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 5 | 2 | 28 | 1 | 71 | 1 | 136 | 1 |
| 7 | 3 | 32 | 1 | 73 | 1 | 138 | 1 |
| 9 | 1 | 35 | 1 | 77 | 1 | 148 | 1 |
| 10 | 2 | 36 | 2 | 78 | 1 | 168 | 1 |
| 11 | 2 | 37 | 1 | 82 | 1 | 170 | 1 |
| 12 | 1 | 40 | 1 | 85 | 1 | 188 | 1 |
| 13 | 2 | 45 | 1 | 89 | 1 | 198 | 1 |
| 14 | 2 | 46 | 3 | 98 | 1 | 207 | 1 |
| 15 | 1 | 47 | 1 | 105 | 1 | 215 | 2 |
| 16 | 1 | 48 | 2 | 107 | 1 | 225 | 1 |
| 18 | 2 | 51 | 2 | 109 | 1 | 251 | 1 |
| 20 | 3 | 58 | 1 | 110 | 1 | 362 | 1 |
| 23 | 2 | 65 | 1 | 117 | 1 | 407 | 1 |
| 24 | 1 | 67 | 1 | 128 | 1 | 453 | 1 |
| 26 | 1 | 69 | 2 | 130 | 1 | 701 | 1 |
| 27 | 2 | 70 | 1 | 134 | 1 | 1,274 | 1 |

Total of 8,440 capsules on 83 plants. Average 102±12·5.

As with *L. spuria*, the flowering and fruiting is prolonged, and the quantity of fruits produced depends to a considerable degree on the length of the growing season and the favourability of the autumn weather.

The seeds per capsule were counted in 105 capsules, as shown in Table LI.

TABLE LI. VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *LINARIA ELATINE* MILL.

| Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules |
|---|---|---|---|---|---|---|---|
| 4 | 1 | 10 | 7 | 16 | 9 | 22 | 5 |
| 5 | 0 | 11 | 2 | 17 | 7 | 23 | 5 |
| 6 | 2 | 12 | 1 | 18 | 7 | 24 | 7 |
| 7 | 0 | 13 | 2 | 19 | 13 | 25 | 3 |
| 8 | 1 | 14 | 9 | 20 | 8 | 26 | 1 |
| 9 | 2 | 15 | 5 | 21 | 7 | 27 | 1 |

Total of 1,847 seeds in 105 capsules. Average 17·59±0·32.

They contained 1,847 seeds, giving an average of 17·59±0·32 seeds per capsule ($\sigma$ 4·84; S.E.M. 0·48).

The average seed output is therefore 1,798±252 seeds per plant, or approximately between fifteen hundred and two thousand seeds per plant. The average weight of a seed is 0·0004 gm., so that the average weight of seed per plant would be about 0·72 gm.

Of the three annual species considered the average seed production is then as follows:

| | |
|---|---|
| *Linaria minor* | 1,848–2,488 seeds |
| ,, *elatine* | 1,546–2,050 ,, |
| ,, *spuria* | 1,839–2,725 ,, |

Having regard to the wide range in capsule production of the two prostrate species it may well be that the differences in seed production indicated have no significance; but whilst the three species may well be of the same order of productivity it is probable that the viability of the seeds is greatest for *L. minor* and least for *L. spuria.*

As shown by the accompanying maps (Fig. 23) the distribution of these three species in Great Britain and Ireland is widest for *L. minor* and most restricted for *L. spuria.* The former has in all probability the highest reproductive capacity, although exact germination data are not available. Owing to its restriction to open habitats the small size of the seeds which favours their dispersal is no appreciable handicap.

Comparatively few data are available for the perennial species of *Linaria,* but they are sufficient to indicate the approximate magnitude of their seed production.

Yellow Toadflax, *Linaria vulgaris* Mill.

It is only occasionally that it is possible to obtain satisfactory determinations of fruit production by this species, as the limits of the individual are often not determinable. In the small number of specimens where this was possible the number of fruits ranged from 374 to 530, with an average of 440±31·4 fruits. The number of seeds was counted in twelve capsules, and ranged from 25 to 107, with an average of 71±3·7 ($\sigma$ 19·2; S.E.M. 5·6). As many as 166 seeds in a capsule were found by Darwin (1876, p. 88) to result from cross-fertilization, but an average of only 23·6 seeds per capsule as a consequence of self-fertilization. The average seed output would appear to be about 31,386±3,827 or roughly between 28,000 and 35,000 seeds per plant per annum. As an outcome of the vegetative spread of this species all the plants of Yellow Toadflax in an area might be merely clones of one original seedling. Under these conditions we should expect the seed yield to be about one-third of that from cross-pollination of clones from distinct seedlings. The viability of the seeds in this country is apparently low, especially in wet summers. Various germination tests carried out on fresh seeds yielded below 1 per cent of seedlings. Kinzel, on the continent, however, obtained 15 per cent germina tion, whilst Mitchell, in America (1926, *Bot. Gaz.*, 81, p. 108) obtained from 15 to 24 per cent (average 20 per cent) in the light and from 0 to 9 per cent in


FIG. 23. Maps showing the distribution of five British species of Toadflax (*Linaria* species).

darkness. According to Anneliese (1927) the seeds of this species have to pass through a pronounced rest period before germination will begin. Its absence from the north-west of Scotland (*cf.* map) and its rarity in the wetter parts of Ireland lend support to the view that continental rather than oceanic conditions favour the seed production of this species. It has a remarkably prolific means of vegetative multiplication (Fig. 31) by adventitious shoots from the roots (*cf.* Salisbury, E. J., 1929, *Jour. Ecology*, XVII, p. 214). The distribution of the species and its local abundance suggests rather poor dispersal but efficient multiplication, once colonization has taken place, and this is probably an example of a species whose maintenance in the northern and western extremes of its range has depended rather on successful vegetative multiplication than upon seed production. The very large seed output compared with the annual species is a striking feature.

Striped Toadflax, *Linaria repens*

This perennial species extends also by vegetative means, though not so markedly as *L. vulgaris*. The fruit production was determined for seven plants only, and ranged from 118 to 732 capsules per plant. The average was $249 \pm 50$ capsules per plant ($\sigma$ 200; S.E.M. 75·7). The seeds were counted in eleven capsules, and ranged from 10 to 31. The average was $21{\cdot}2 \pm 1{\cdot}0$ seeds per capsule ($\sigma$ 5·3; S.E.M. 1·6). The average seed output is therefore $5{,}328 \pm 1{,}309$, or roughly between four thousand and six thousand six hundred seeds per plant per annum. Here again the seed output is appreciably greater than for either of the annual species.

Purple Toadflax, *Linaria purpurea*

On the few specimens available the capsules ranged in number from forty to seven hundred and twenty-six. The mean for seven plants was 284 capsules $\pm 66$ ($\sigma$ 257·3; S.E.M. 99) and seeds per capsule $15 \pm 0{\cdot}61$. The mean seed output is therefore between 4,400 and 7,770 seeds per plant. Here again the high seed production compared with the annual species must be noted; but attention should be called to the erratic fruiting of this species, which, although usually flowering profusely, often fails to produce more than a few fruits. This accounts for the high value of $\sigma$, even with this small number of specimens. The average seed weight is 0·000106 gm., or a total weight of seeds per plant per annum of 0·645 gm.

Ivy-leaved Toadflax, *Linaria cymbalaria*

The seeds were counted in seventeen capsules of this species, and ranged from 15 to 42, distributed as follows: 15 (1), 24 (1), 26 (1), 27 (3), 29 (1), 30 (2), 33 (1), 34 (4), 35 (2), 42 (1). The mean number of seeds per capsule is therefore 30 $(30{\cdot}35) \pm 0{\cdot}97$ ($\sigma$ 5·8; S.E.M. 1·45). Germination averages about 61 per cent.

The capsule number per plant is often high, but was not determined owing to the difficulty of ascertaining the limits of individuals.

The distribution of the Ivy-leaved Toadflax (*Linaria cymbalaria*) is a striking instance of the spread of an introduced species in artificial habitats.

Originally a garden escape, the first record dates from 1640, and it is now found on old walls throughout Great Britain and Ireland. It is probable that it owes its spread in no small degree to human agency. In Ireland Lloyd Praeger (1934, 420) describes how this species has "forsaken its usual mural habitat and is abundant on the rough limestone rocks" near Lough Gill. Like other calcicole species, not only of plants but of animals (*e.g.* Clausilia spp.) the mortar joints of old walls provide a suitable artificial extension of the natural habitats.

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Considering the genus as a whole, it can be said that the frequency of the individual species is roughly parallel to their respective seed outputs, but that their abundance is for the annual species perhaps proportional to their reproductive capacities, whilst for the perennial species it probably corresponds to the reproductive capacity only to a minor degree and mainly perhaps to the rate of vegetative spread.

# XV

# THE GENUS *VERBASCUM*
# MULLEINS

The British species of this genus afford comparison between the biennial, or sometimes annual, types, such as *V. Thapsus*, *V. Lychnitis*, which are monocarpic, and the perennial, polycarpic species *V. nigrum*. These three species, moreover, present three degrees of frequency. *V. Thapsus* is present alike in England, Scotland, and Ireland, the respective comital and vice-comital frequencies being 100 per cent, 68 per cent, and 92 per cent. Neither of the other two species occur, except as casuals, in either Scotland or Ireland, but whereas *V. nigrum* has a comital frequency in England of 70 per cent that of *V. Lychnitis* is only 24 per cent and is almost always rare in contrast to *V. nigrum*, which in some areas is fairly common.

Mullein, *Verbascum Thapsus* L.

The observed range in number of capsules on 37 plants of this species was from 33 to 1,856 fruits per plant, with an average of 226$\pm$42 ($\sigma$ 380; S.E.M. 63).

The seeds were counted in sixteen capsules and totalled 9,535, with a range of from 370 to 949 seeds per capsule. The average number of seeds was 596$\pm$30 ($\sigma$ 180; S.E.M. 45). The average seed output is therefore about 136,000$\pm$32,000 seeds per plant. The seeds (Fig. 21, p. 95) weigh 0·00009 gm.

According to Lehmann the germination in light is between 71 and 75 per cent and from 63 to 65 per cent in the dark. Gardener (1921, *Bot. Gaz.*, p. 253) obtained from 53 to 94 per cent germination in the light and only from 0 to 1 per cent in the dark. The average germination under normal conditions would appear to be about 80 per cent, so that the potential average reproductive capacity would be approximately 108,800$\pm$25,600 offspring per plant. Under favourable light conditions, as in coppiced areas in woodlands, very large numbers of individuals of *V. Thapsus* may develop, and a high proportion survive to maturity; indeed, in one such area, the number of flowering specimens was fifty-two in ten square metres (*cf.* Plate III). *V. Thapsus* affords a very striking example of a species of which the population is subject to great and frequent fluctuations, although the average number over a period of years remains comparatively constant. The latter feature is, however, of far less biological significance than these population changes, which emphasis on the average population would obscure.

The abundant flowering specimens of *Verbascum Thapsus*, which may occupy coppiced areas in woodlands in the second year after the undergrowth has been cut down (*cf.* Plate III), must either have originated from dormant seeds or from seeds produced by the small number of marginal specimens. The latter explanation appears the less likely both from the numbers of individuals and from their distribution. H. J. Oosting and M. E. Humphreys (1940) have

recently furnished evidence that the seeds of this species are probably still viable when buried in the soil for a period of 58 years.

White Mullein, *Verbascum Lychnitis*

Twenty-five plants of this species were studied for capsule production. The number of these ranged from 132 to 3,651 fruits per plant, with an average of 960±97 ($\sigma$ 728; S.E.M. 145). The seeds were also counted in twenty capsules and totalled one thousand eight hundred and forty-four. The number of seeds per capsule ranged from 67 to 153, with an average of 92·2±3·1 ($\sigma$ 21·3; S.E.M. 4·7). The average seed output is therefore 88,211 ±5,968 or, in round figures, between 82,000 and 94,000 seeds per plant.

According to Kinzel the germination of this species in light is only 38 per cent. If we use this figure the potential reproductive capacity has an average value of 34,435±5,182, or roughly between 29,000 and 39,000 offspring.

The average weight of a seed of *V. Lychnitis* is 0·0001265 gm., so that the average weight of viable seed per plant would be 4·2 gm. The average weight of a seed of *V. Thapsus* is 0·00009 gm., so that the average weight of viable seed per plant would be just over 12 gm. It is obvious from the distribution of these species in the British Islands that *V. Lychnitis* is less tolerant of a wide range of edaphic and climatic conditions than *V. Thapsus*, so that it is reasonable to assume that the mortality of the former species is appreciably greater than that of the latter, which might lead us to expect a higher reproductive capacity. The reverse is the actual condition, so it would appear that here, as in other instances considered, frequency and reproductive capacity exhibit a certain degree of parallelism.

Black Mullein, *Verbascum nigrum* L.

Twenty-two plants of this species yielded from 198 to 3,300 capsules per plant, with an average of 1,108±131 ($\sigma$ 928; S.E.M. 197).

The seeds were counted in sixteen capsules and varied in number from 29 to 87, with an average of 62·7±2·2 ($\sigma$ 13·5; S.E.M. 3·37). The average seed output from these data is 70,562±9,849 seeds per plant per annum, or about 60,000 to 80,000 seeds.

According to Kinzel the germination in light of this species is only 8 per cent, which would give an average reproductive capacity of 5,742 potential offspring per annum. But, from my own experience, this percentage germination of Kinzel's is probably much too low as an average. *V. nigrum* is a long-lived perennial, and one moreover which it is difficult to kill by frequent cutting of the overground organs, so that whilst its reproductive capacity cannot compete with the prodigious fertility of *V. Thapsus* it is probably, even in a single season, not so much inferior to *V. Lychnitis* as to surprise us that its frequency is the greater. At the same time the high productivity in the one year of *V. Lychnitis* accounts for its manifesting marked fluctuations of population like *V. Thapsus*. Though usually very rare, and represented by a few individuals, very large colonies of *V. Lychnitis* infrequently occur in Southern England.

# XVI

# REPRODUCTION IN RELATION TO HABITAT AND CONDITIONS OF COLONIZATION

It is obvious that, apart from the competition factor, the facility of colonization is greatest when the habitat is completely open. The degree to which different types of habitat afford open conditions where colonization can take place is thus of the first importance. Even amongst species of closed or semi-closed communities reproduction from seed is to a considerable degree dependent upon the occurrence of less shaded areas, although partial shade is often a favourable factor for their establishment by reason of the greater handicap it imposes upon possible competitors of open habitats.

Amongst the species of open habitats we shall find it useful to distinguish between two categories, viz.:

1. Species of continuously open habitats.
2. Species of intermittently open habitats.

The term " continuously open habitat " is here applied to two types of environment. There are the artificial habitats provided by cultivated ground, waysides, etc., where the activities of man maintain the open character of the habitat, and which are mainly occupied by species that have their natural occurrence in habitats of the second type to be mentioned, or, perhaps in a few instances, species which may have arisen since neolithic man initiated agricultural pursuits, and are as truly domestic as the Wheat or the Banana.

The second type of continuously open habitat is the natural one, where the uninterrupted continuity may be either temporal or spatial. Uninterrupted continuity in space is seen in deserts where the climatic or edaphic conditions, or both, inhibit any successional advance; though it must be recognized that some desert habitats, despite being continuously open, may, by reason of lack of continuity in the minimum conditions necessary for growth, belong to our second category.

To the natural continuously open habitats belong also those in which the continuity is temporal. Such are the younger stages of sand dunes, moraines, etc., which though themselves passing gradually into closed habitats are normally in juxtaposition to embryonic phases, which, by their continual renewal, perpetually maintain the temporal continuity of the open habitat, although the actual space occupied is perpetually changing.

In contrast to the habitats which always provide open conditions where seedlings can germinate are those where the open character is intermittent. Such are provided naturally by the light gaps in woodlands when a dominant tree dies, or artificially on a larger scale where felling or coppicing has taken place. Fires, natural and artificial, floods, and landslides also furnish habitats of this class.

The annual fluctuations in water level of lakes and ponds provide a zone that is often only partially open. The conditions, though seasonally discontinuous, are annually continuous, and, unless the changes of level are considerable, such species as the perennial *Alopecurus geniculatus* may be permanently in possession. But the larger shrinkages, due to seasons of abnormally low rainfall, by the exposure of unoccupied mud provide intermittently open habitats where species far less tolerant of competition occur, including the more characteristic species of drying mud. Here, it is pertinent to note we find the rare grass *Alopecurus fulvus*, an annual and closely allied congener of *A. geniculatus*, sometimes in astonishing profusion.

The intermittently available habitats just cited are due to a periodicity, usually quite irregular in character, in the physical environment. But it should also be noted that there may well be a further class of such periodic habitats that are the outcome of direct physiological changes not brought about by obvious modifications of the physical environment.

There are some species, such as *Chlora perfoliata* and several of the terrestrial Orchids (*e.g. Orchis morio*, *Ophrys apifera*), which when they appear in large numbers in any area usually exhibit an abrupt decline in numbers or even complete disappearance, and may not reappear in the same area despite the vast numbers of seeds that must have been shed on to the soil and the apparently unchanged character of the environment. One possibility is that particular climatic conditions that only recur at infrequent intervals are necessary for establishment, but it seems far more probable that the explanation is of a more direct physiological character, such as unfavourable conditions for the mycorrhizal fungus. The fact that the more permanent constituents of the vegetation appear to remain equally vigorous would suggest that it is no mere exhaustion of any of the major nutrients, though it might perhaps be an outcome of diminution of certain trace elements, the demand for which is known to vary in respect to different species.

The phenomenon is not, it would appear, confined to mycorrhizal species, for the remarkable rise to dominance of *Elodea canadensis* and *Mimulus Langsdorfii* on their first appearance in new habitats, followed by as spectacular a decline, is probably one of a similar character. In particular localities I have observed comparably rapid increase, followed by abrupt decline or even complete disappearance, with respect to *Bidens cernua* and *Utricularia vulgaris*. In one such instance attempts were made to re-establish *U. vulgaris*, in a pond where it had died out completely after a season of astounding vigour and abundance, but without success. Such phenomena clearly challenge investigation and constitute a stimulating parallel to certain types of epidemic disease.

The recognition that certain species are characteristic of natural habitats that are only intermittently available is important, and it is not entirely an academic concept that the monocarpic perennial, and in some degree the biennial also, is in the same category.

## (A) Reproduction in Species of Continuously Open Habitats

### SAND DUNE SPECIES

*Hutchinsea petraea* Br.

Specimens of this species were examined on the sand dunes on various parts of the Welsh coast. Thirty-six specimens were studied for the number of fruits, which ranged from 6 to four hundred and ten. The average number was $99 \pm 10{\cdot}4$ ($\sigma$ 93·4; S.E.M. 15·56). The individual fruits contain from three to four seeds, more usually the latter number, so that the average seed output per plant would be between 354 and four hundred and thirty-eight. Even the largest specimen encountered would not have yielded more than about 1,600 seeds.

The actual number of fruits observed was as follows: 6, 8, 11, 15, 17, 18, 23, 24, 26, 38, 40, 40, 41, 44, 45, 47, 53, 59, 76, 79, 83, 90, 91, 97, 120, 120, 122, 130, 178, 180, 180, 220, 240, 252, 320, 410. From these it will be seen that two-thirds of the specimens bear less than the average number of fruits.

*H. petraea* is a characteristic plant of calcareous dunes and also of limestone rocks, where it is equally associated with permanently open habitats. H. S. Thompson (1920, *Jour. Bot.*, p. 252) estimated that a very large plant from Clifton bore 6,600 seeds.

Whitlow Grass, *Erophila* (*Verna*) *Praecox* DC.

Ninety-four specimens of this species from Llanbedr Dunes were examined for fruit production, and the details are given in Table LII.

TABLE LII. FRUIT PRODUCTION IN *EROPHILA PRAECOX* DC.

| Number of pods | Number of individuals | Number of pods | Number of individuals | Number of pods | Number of individuals |
|---|---|---|---|---|---|
| 1 | 7 | 7 | 5 | 16 | 1 |
| 2 | 8 | 8 | 6 | 17 | 2 |
| 3 | 15 | 9 | 3 | 19 | 1 |
| 4 | 14 | 10 | 2 | 25 | 1 |
| 5 | 15 | 11 | 2 | 27 | 1 |
| 6 | 7 | 13 | 3 | 32 | 1 |

Total of 585 pods on 94 plants.

The average number of pods per plant is thus six ($6{\cdot}2 \pm 0{\cdot}37$), with a standard deviation of 5·4 and S.E.M. 0·55.

The seeds were counted in twenty pods and ranged in number from 14 to 31, with an average of 22 seeds per pod ($21{\cdot}8 \pm 0{\cdot}6$; $\sigma$ 4·9; S.E.M. 1·0). The average seed output is therefore $135 \pm 12$ seeds per plant, or approximately between 120 and 150 seeds.

Whitlow Grass, *Erophila* (*Verna*) *Boerhaavii* Dum.

A second species of *Erophila* from the same locality distinguished by the possession of stellate hairs and dentate leaves and more numerous ovules in the ovary than the foregoing, in which the leaves were entire and with simple or bifurcate hairs, I have taken to be *E. Boerhaavii* Dum.

Only twenty-five specimens were obtained of this species, and these bore

from 4 to 39 pods, as follows: 4 (2), 7(1), 8 (1), 10 (2), 11 (1), 12 (3), 13 (1), 14 (1), 15 (2), 16 (1), 18 (2), 21 (1), 24 (1), 26 (1), 27 (1), 33 (3), 39 (1). The average is thus 17 pods per plant (17·4±1·2; $\sigma$ 9·5; S.E.M. 1·9).

The seeds were counted in fifteen pods, and numbered from 24 to 40, with an average of 32±0·82 ($\sigma$ 4·72; S.E.M. 1·24).

The average seed output is therefore 557±52, or approximately between 500 and 600 seeds per plant.

*Cerastium semidecandrum* L.

Seventy-seven plants of this species were examined for fruit number, which ranged from one capsule to 72 per plant. The seeds were counted in twenty-five capsules and varied in number from 8 to 30. The details are furnished in Table LIII.

TABLE LIII. VARIATION IN CAPSULE NUMBER AND SEEDS PER CAPSULE OF *CERASTIUM SEMIDECANDRUM* L.

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 11 | 4 | 21 | 3 | 33 | 1 |
| 2 | 1 | 12 | 1 | 22 | 3 | 37 | 1 |
| 3 | 0 | 13 | 6 | 23 | 0 | 38 | 1 |
| 4 | 1 | 14 | 2 | 24 | 1 | 39 | 1 |
| 5 | 2 | 15 | 2 | 26 | 1 | 42 | 1 |
| 6 | 8 | 16 | 2 | 27 | 1 | 45 | 1 |
| 7 | 7 | 17 | 1 | 28 | 1 | 59 | 1 |
| 8 | 3 | 18 | 0 | 29 | 1 | 72 | 1 |
| 9 | 5 | 19 | 5 | 31 | 1 | | |
| 10 | 5 | 20 | 0 | 32 | 1 | | |

Total of 1,210 capsules on 77 plants.

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|---|---|---|---|
| 8 | 2 | 14 | 2 | 20 | 0 | 26 | 2 |
| 9 | 2 | 15 | 1 | 21 | 1 | 27 | 1 |
| 10 | 1 | 16 | 3 | 22 | 1 | 28 | 0 |
| 11 | 0 | 17 | 1 | 23 | 0 | 29 | 0 |
| 12 | 2 | 18 | 1 | 24 | 0 | 30 | 1 |
| 13 | 1 | 19 | 2 | 25 | 1 | | |

Total of 432 seeds in 25 capsules.

The average number of capsules per plant was 16·88±0·82 ($\sigma$ 6·2; S.E.M. 1·24), and the average number of seeds per capsule 15·7±0·9 ($\sigma$ 12·7; S.E.M. 1·4). From these data the average seed output would be 256±28 seeds per plant, or approximately between 240 and 290 seeds.

*Hypochoeris glabra* L.

This species is a plant both of dunes and open sandy and gravelly places. Unlike its British congeners it is annual and possesses dimorphic fruits. The

two types of fruits, which occur together in the same capitula and are associated with the disk and ray florets respectively, apparently have about the same viability. The germination, according to Becker (1912, *Beihefte Bot. Centralbl.*, 29) is 93 per cent for the disk fruits and 100 per cent for the marginal ones.

Twenty-six dune plants of this species were examined and yielded 289 capitula, as follows: 2 (1), 3 (3), 4 (1), 7 (2), 8 (5), 9 (2), 10 (1), 12 (2), 13 (1), 14 (1), 15 (1), 16 (1), 20 (1), 21 (1), 22 (2), 25 (1). An average of $11{\cdot}1 \pm 0{\cdot}8$ capitula per plant ($\sigma$ 6·4; S.E.M. 1·2).

The fruits per capitulum ranged from 7 to 20, as follows: 7 (1), 8 (4), 9 (2), 10 (4), 11 (2), 12 (5), 13 (2), 14 (1), 15 (1), 17 (2), 20 (4). The average for the twenty-eight fruiting heads was thus $12{\cdot}4 \pm 0{\cdot}5$ ($\sigma$ 4·0; S.E.M. 0·75). The average seed output was therefore $138 \pm 16$, or approximately between 120 and 150 achenes per plant. From Becker's data it would appear that the average reproductive capacity would be about 130 potential offspring per plant.

Sea Rocket, *Cakile maritima* Scop.

Only a few plants of this species were examined, but one plant above the average in size yielded 5,628 fruits. Each fruit contains two seeds, which were found by Becker (*loc. cit.*) to differ in weight, the upper being 0·0093 gm. in weight and the lower 0·0085 gm. The respective germinations recorded by the same investigator were: upper seeds 52–74 per cent, lower seeds 54–70 per cent. We may take the average germination as being about 62 per cent, so that a large plant would yield about 6,300 viable seeds. The average reproductive capacity may perhaps not exceed three thousand.

Scented Stork's-Bill, *Erodium moschatum* L.

Thirteen plants of this dune species yielded a total of 70,790 schizachenes, the number for the individual plants varying from 550 to eight thousand one hundred and sixty-five. The average was $5{,}445 \pm 442$, or approximately between 5,000 and 5,900 seeds per plant ($\sigma$ 2,387; S.E.M. 663). Germination is normally high and probably averages about 95 per cent, which would imply an average reproductive capacity of about 5,000 potential offspring per plant. A biennial or winter-annual of which the mortality in severe winters is high. (For distribution map *cf.* Salisbury, 1939, p. 346.)

*Medicago minima* Desr.

The number of pods per plant ranged from 14 to 109, with an average of $40 \pm 7{\cdot}5$. The seeds were counted in fifty pods and showed the following distribution: 2 seeds (7), 3 (17), 4 (12), 5 (10), 6 (4); an average of $3{\cdot}74 \pm 0{\cdot}1$ ($\sigma$ 1·16; S.E.M. 0·16).

The average seed output is then $150 \pm 32$, or roughly between 120 and 130 seeds per plant. Tests of the germination of the seeds indicate an average of about 45 per cent.

Hence the average reproductive capacity of *Medicago minima* is probably about sixty-seven potential offspring per plant.

In addition to the species of dune annuals just considered we have already furnished data respecting the reproduction of *Saxifraga tridactylites* and *Cardamine hirsuta*. The latter, when growing on dunes, had an average seed output of 98 seeds per plant, whilst the former showed an average output of 1,106±98 seeds per plant.

From all the above data it will be apparent that the seed production of dune annuals is not in general high, the largest reproductive capacity being observed in *Cakile maritima;* but even in this species the number of seeds is small in comparison with the size of the individual. It is, however, true that most of the dune annuals are of relatively small size compared with those of some other habitats, and therefore *Hyoscyamus niger* was particularly studied, as being a dune species capable of attaining considerable size and found also in other habitats that may in general be regarded as permanently open in the sense indicated above. Some of the specimens were from dune habitats and others from light disturbed sandy soil.

Henbane, *Hyoscyamus niger* L.

The data respecting the capsule production of 458 plants obtained during three different seasons is furnished in Table LV and Fig. 24. The average for all these is 19±1·18 capsules per plant. The following summary for the three separate seasons is of interest as showing that the average production of capsules per plant shows no significant difference despite marked climatic distinctions, since the year 1936 was characterized by a very wet summer deficient in sunshine whereas the summer of 1939 was dry and sunny. It may be noted, however, that though the means for numbers of capsules per plant show no statistically significant difference the sequence of increasing means corresponds with the sequence of increasing sunshine. The standard deviation is greatest for the wettest season, a feature accounted for by the fact that the greater rainfall has resulted in the survival of a greater number of depauperate plants and the development of larger specimens than in the dry summer, which, though more favourable to fruit formation is less so to growth. The number of seeds per capsule for 1936 varied from 180 to 511,

TABLE LIV. SUMMARY OF DATA REGARDING CAPSULE PRODUCTION BY *HYOSCYAMUS NIGER* L. IN DIFFERENT SEASONS

| Year | Mean number of capsules | $\sigma$ | S.E.M. | Difference of means | | S.E.D. | S.E.D.×3 |
|---|---|---|---|---|---|---|---|
| 1936 | 17 | 23·08 | 1·81 | '38–'36 | 1·2 | 2·51 | 7·53 |
| 1938 | 18·2 | 20·45 | 1·75 | '39–'38 | 2·9 | 2·50 | 7·50 |
| 1939 | 21·1 | 22·7 | 1·79 | '39–'36 | 4·1 | 2·54 | 7·62 |

and in 1939 from 180 to 513; but though the mean for the former year was 330 seeds per capsule and for the latter 362, the standard errors being 12·5 and 18·7 respectively, the difference is not significant. The number of seeds were counted in 74 capsules (40 in 1936, 9 in 1938, and 25 in 1939) and totalled 24,420, an average of 330±7 ($\sigma$ 90·5; S.E.M. 10·52). The average seed output is thus 6,278±522 per plant, or approximately between 5,700 and 6,800 seeds. The largest plant examined would probably have produced

TABLE LV. VARIATION IN CAPSULE PRODUCTION OF *HYOSCYAMUS NIGER*

| Number of capsules | Number of individuals year 1936 | Number of individuals year 1938 | Number of individuals year 1939 |
|---|---|---|---|
| 1 | 3 | 3 | 8 |
| 2 | 6 | 11 | 12 |
| 3 | 12 | 13 | 9 |
| 4 | 15 | 11 | 6 |
| 5 | 4 | 9 | 5 |
| 6 | 11 | 7 | 11 |
| 7 | 9 | 6 | 5 |
| 8 | 11 | 7 | 8 |
| 9 | 13 | 7 | 6 |
| 10 | 6 | 1 | 3 |
| 11 | 5 | 2 | 6 |
| 12 | 2 | 3 | 3 |
| 13 | 7 | 1 | 2 |
| 14 | 1 | 2 | 4 |
| 15 | 4 | 1 | 1 |
| 16 | 3 | 4 | 3 |
| 17 | 3 | 2 | 4 |
| 18 | 2 | 2 | 2 |
| 19 | 2 | 1 | 3 |
| 20 | 4 | 2 | 1 |
| 21 | 3 | 2 | 4 |
| 22 | 2 | 1 | 2 |
| 23 | 3 | 2 | 8 |
| 24 | 2 | 2 | 3 |
| 25 | 2 | 2 | 1 |
| 26 | 0 | 2 | 1 |
| 27 | 1 | 0 | 3 |
| 28 | 3 | 1 | 4 |
| 29 | 1 | 1 | 0 |
| 30 | 0 | 2 | 2 |
| 31 | 2 | 0 | 0 |
| 32 | 0 | 1 | 2 |
| 33 | 1 | 1 | 0 |
| 34 | 1 | 0 | 0 |
| 35 | 1 | 0 | 0 |
| 36 | 2 | 0 | 2 |
| 37 | 0 | 0 | 1 |
| 38 | 1 | 1 | 2 |
| 39 | 1 | 0 | 0 |
| 40 | 0 | 4 | 0 |
| 41 | 0 | 0 | 1 |
| 42 | 1 | 0 | 0 |
| 43 | 1 | 0 | 1 |
| 44 | 1 | 0 | 1 |
| 47 | 0 | 0 | 1 |
| 50 | 1 | 0 | 1 |
| 52 | 0 | 0 | 1 |
| 54 | 0 | 0 | 1 |
| 56 | 0 | 0 | 1 |
| 57 | 1 | 0 | 0 |
| 58 | 0 | 0 | 1 |
| 60 | 0 | 0 | 1 |

TABLE LV. VARIATION IN CAPSULE PRODUCTION OF *HYOSCYAMUS NIGER—Continued*

| Number of capsules | Number of individuals year 1936 | Number of individuals year 1938 | Number of individuals year 1939 |
|---|---|---|---|
| 61 | 0 | 0 | 1 |
| 62 | 1 | 0 | 0 |
| 67 | 1 | 0 | 0 |
| 68 | 1 | 0 | 1 |
| | also 87, 127, 133, and 180 capsules | | also 72, 77, 90, 91, 100, 101, 102, and 105 capsules |

| | | | | |
|---|---|---|---|---|
| 1936: | Total of 2,753 capsules | on 162 plants. | Average | $17{\cdot}0 \pm 1{\cdot}2$ |
| 1938: | „ 2,476 „ | 136 „ | „ | $18{\cdot}2 \pm 1{\cdot}2$ |
| 1939: | „ 3,382 „ | 160 „ | „ | $21{\cdot}1 \pm 1{\cdot}2$ |

about 60,000 seeds. Two strains occur on dunes, namely the annual and biennial. Germination takes place in the early summer, and from experiments by F. Doerfel (1930) the seeds of *Hyoscyamus* and *Datura* alike respond best to alternating temperatures, the former to a short period of low temperature and a long period of high temperature, the latter to a long exposure to low temperature and a short exposure to high. This feature may in part account for the very pronounced fluctuations in population numbers.

The pioneer species of the salt marsh occupy, in a similar manner to those of the sand dune, a habitat which in time, if not in space, is permanently open. Of these salt marsh species the most characteristic are *Salicornia dolichostachya*, the pioneer species upon the muddier types of salt marsh, and *Salicornia ramosissima*, the pioneer upon the more sandy types. A well-grown specimen of the latter species yielded about 3,000 seeds, whilst one of the former yielded 1,440 seeds and a very large plant 7,000. The average seed output for these would undoubtedly be below the figures named.

Although shingle beaches afford permanently open habitats they are to a great extent only intermittently available so far as colonization by seed is concerned. Owing to their coarse texture the development of seedlings on shingle is to a considerable degree dependent upon the distribution by storms of finer material, such as sand, silt, and organic debris, which temporarily occupies the superficial interstices and thus, until washed down to lower levels, forms a suitable nidus for the germination of the accompanying seeds.

Hence it is that the occurrence of many shingle species is apt to be markedly intermittent, a feature notably exemplified by *Rumex crispus v. trigranulatus* and *Glaucium luteum*, which will occupy a section of a shingle beach in large numbers. When the adults perish, however, it may be years before the same area is again occupied by these species, meanwhile other areas may be densely colonized. There is, however, one shingle beach species which always occupies areas where the interstices are filled sufficiently to provide a permanently suitable habitat of an open character, namely *Statice binervosa*. A large plant of this species will produce between 800 and 900 fruits, and 330 were counted from a medium-sized specimen. Many individuals are, however, quite small, and four such dwarf plants yielded from 17 to 103 fruits. Very large specimens will produce over 1,000 fruits, but it is clear from these data

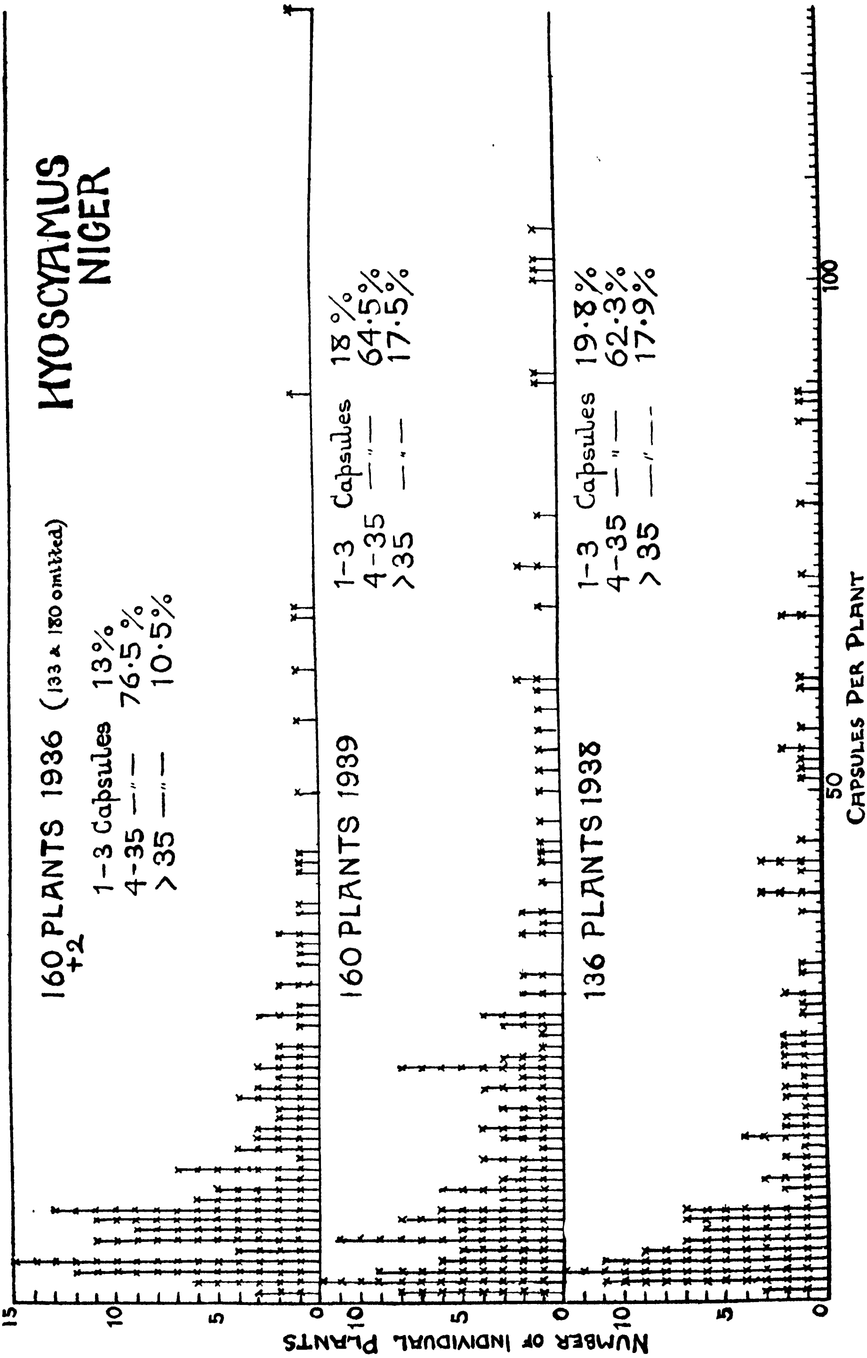



FIG. 24. Frequency distribution graphs for the number of capsules per plant of *Hyoscyamus niger* for three different seasons.

that the average seed output is comparatively small, probably under three hundred.

*Additional Shingle and Dune species*

There are a considerable number of species which, owing to the mode of their growth in the adult condition, are not delimitable as separate individuals, and this is especially true of certain shingle-beach, dune, and pasture species. Although, as a consequence of their mode of growth, the assessment of their output of seeds cannot be determined on the basis of the individual, it is possible in certain instances to obtain useful data with respect to their output per unit area. Such a method of assessment has a measure of validity for those species which occur in pure stands as, for instance, *Silene maritima* and *Honkenya peploides* on the shingle beach, and also for plants in mixed stands where there is a measure of uniformity, with respect to the density of occurrence and the nature of the competitors as, for example, *Convolvulus soldanella* on dune systems growing in association with *Ammophila arenaria.* But for many pasture species, where the density is very variable and the competing species are several, or even numerous and in diverse proportions, it is doubtful if the many variables permit of estimates that have more than a purely local validity.

Sea Purslane, *Honkenya peploides* Ehrh.

This species was studied on the shingle at Blakeney Point, Norfolk. It there occurs both on shingle and on shingle with a considerable admixture of sand, forming almost pure mats of either dense or open growth, apparently depending in large part upon the extent to which the locus is stable or partially mobile. In the latter condition the plants are fed with a limited supply of fine shingle and organic debris which the shoots themselves arrest and stabilize. If the organic supplies are considerable a luxuriant mat may develop which is largely vegetative, perhaps as a result of the disturbance of the Carbohydrate-Nitrogen balance, whilst at the other extreme completely stabilized shingle is usually also accompanied by a poor seed output, probably as an outcome of inadequate nutrition. The following data were obtained from areas of 100 sq. cm. each, situated in both stable and mobile conditions.

TABLE LVI. SEED-POD PRODUCTION BY *HONKENYA PEPLOIDES* PER 100 SQ. CM.

| Locus | Habitat | Number of pods | Average number of seeds | Average weight of one seed in gm. |
|---|---|---|---|---|
| A | Stable shingle | 114 | | |
| B | " " | 117 | 3·2 0·11 | 0·015 |
| C | " " | 162 | | |
| D | Stable sandy shingle | 31 | 3·9 | |
| E | " " " | 35 | 3·3 | 0·0144 |
| F | " " " | 49 | 2·7 | |
| G | " " " | 57 | 5·5 | 0·0134 |
| H | Mobile shingle | 184 | 6·3 | 0·0138 |
| J | Sandy mobile shingle | 38 | 6·0 | 0·0163 |
| K | Mobile shingle | 76 | 5·8 | |
| L | " " | 46 | 5·9 | 0·0162 |
| M | " " | 108 | 7·4 | 0·0174 |

It will be noted that the highest number of pods per 100 sq. cm., the heaviest seeds, and the largest number of seeds per pod were obtained from mobile shingle. On the other hand, the lowest output of pods, the lightest weight seeds, and lowest number of seeds per pod, were recorded from stable sandy shingle. The presence of sand intermingled with shingle implies a low degree of surface movement which, being insufficient to remove the sand grains, is probably inadequate to maintain the supplies of organic debris.

The beneficial influence of shingle which is not too stable upon seed production is particularly marked when we examine the range of seed number in the capsules from the two types of habitat as shown in the accompanying Table LVII. It will be noted that the mode for the mobile shingle is six seeds

TABLE LVII. VARIATION IN SEED NUMBER PER CAPSULE OF *HONKENYA PEPLOIDES* GROWING ON MOBILE AND STABLE SHINGLE

| | | Number of seeds per capsule | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | | Number of capsules | | | | | | | | | | | |
| Mobile shingle: 312 capsules, | Loc. 1 | 1 | 3 | 4 | 1 | 7 | 8 | 4 | 11 | 9 | 9 | 6 | 2 |
| 2,027 seeds. Average 6·2 | „ 2 | 2 | 3 | 3 | 2 | 4 | 2 | 2 | 7 | 7 | 1 | 2 | — |
| seeds per capsule | „ 3 | 1 | 7 | 5 | 6 | 10 | 10 | 6 | 10 | — | — | — | — |
| | „ 4 | 0 | 1 | 3 | 7 | 12 | 14 | 4 | 7 | 1 | 3 | 1 | — |
| | „ 5 | — | — | 3 | 7 | 12 | 18 | 3 | 6 | 2 | 1 | 1 | — |
| | „ 6 | — | — | 1 | 2 | 15 | 18 | 10 | 4 | — | — | 1 | — |
| Totals | | 4 | 14 | 19 | 25 | 60 | 70 | 29 | 45 | 19 | 14 | 11 | 2 |
| Stable shingle: 262 capsules, | „ 1 | 8 | 10 | 17 | 17 | 11 | 2 | | | | | | |
| 982 seeds. Average 3·748 | „ 2 | 10 | 12 | 4 | 9 | 2 | 1 | 1 | | | | | |
| seeds per capsule | „ 3 | 2 | 12 | 21 | 8 | 4 | 2 | 1 | | | | | |
| | „ 4 | 6 | 12 | 8 | 10 | 8 | 6 | 4 | 1 | 2 | | | |
| | „ 5 | — | 2 | 4 | 9 | 9 | 14 | 8 | 4 | — | 1 | | |
| Totals | | 26 | 48 | 54 | 53 | 34 | 25 | 14 | 5 | 2 | 1 | | |

per capsule, and this is also true for four of the six loci, the other two having modes between eight and ten. For the stable shingle the mode is between three and four seeds, but for the individual loci the modes range from two to six. The mean for the stable shingle is $3{\cdot}748 \pm 0{\cdot}077$ ($\sigma$ 1·87; S.E.M. 0·116), and for the mobile shingle $6{\cdot}2 \pm 0{\cdot}085$ ($\sigma$ 2·3 ; S.E.M. 0·127), a difference of 2·462 with a standard error of 0·17.

For both types of habitat the average number of capsules per 100 sq. cm. was 86·4 and the average number of seeds per capsule 5·1, or a mean of 440 seeds per 100 sq. cm. As many as 800 capsules per 100 sq. cm. have been recorded, however, under exceptional conditions. Miss Adams (F. W. Oliver, 1922) found that the germination was low, namely 0–2 per cent, but it is likely that abrasion of the seeds by shingle is, as Stiles showed for *Lathyrus maritimus*, essential for the proper germination of the seeds of this species, of which seedlings are very rarely seen. The rhizome bears spur shoots and stolons and accessory buds are frequent, and, by means of these, vegetative spread may occur at the rate of from 25 cm. to 84 cm. per annum.

Sea Milkwort, *Glaux maritima* L.

The number of seeds in 107 capsules of this species was 682. The variation in the number of seeds per capsule (Fig. 25) ranged from two to ten as follows:

2 seeds (1), 3 (2), 4 (16), 5 (10), 6 (29), 7 (19), 8 (18), 9 (11), 10 (1). The average number of seeds was 6·37±0·1 ($\sigma$ 1·63; S.E.M. 0·158), which approximates closely to the mode of six seeds per capsule in 500 others.

The range in number of capsules per unit area is extremely varied. The highest number recorded was 908 capsules on an area of one-quarter of a square metre. The lowest was seven capsules on a similar area. The average was 534 or approximately 85 capsules per 100 sq. cm., which would imply some 541 seeds per 100 sq. cm. It is, however, important to realize that *Glaux* has a

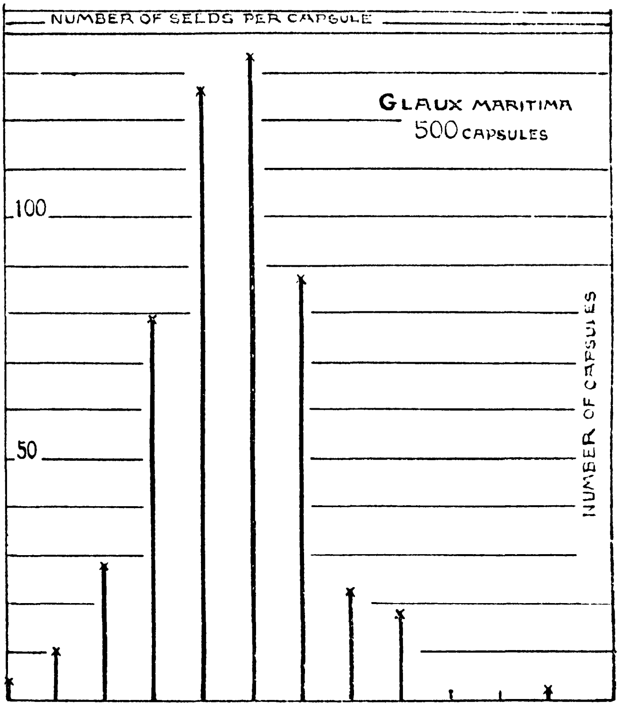



FIG. 25. Diagram showing variation in the number of seeds per capsule in 500 capsules of the Sea Milkwort (*Glaux maritima*). Ordinates represent the number of capsules and abscissae the number of seeds in the capsules.

comparatively rapid rate of vegetative spread, the individual shoots being pseudoannual. If the separate shoots be regarded as the individuals then the observed range was from 0 to 45 capsules per plant.

Sea Convolvulus, *Convolvulus Soldanella* L.

The number of seeds per capsule of this species in 111 capsules was 2·8±0·06. The variation was as follows:

| Locality | Seeds per capsule 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | Number of capsules | | | |
| A | — | 5 | 19 | 36 |
| B | 8 | 9 | 7 | 1 |
| C | 12 | 5 | 6 | 3 |
| Totals | 20 | 19 | 32 | 40 |

The standard deviation was 1·1 and the standard error 0·1.

The fruiting of this species would appear to be somewhat meagre. Counts of the capsules which were made in four areas gave averages of 2·4, 1·8, 3·0, and 3·6 capsules per 100 sq. cm. Thus the areas examined showed an average seed output per 100 sq. cm. of 7·28 seeds. It is possible, however, that in other areas the seed production may be somewhat higher.

If, however, seed production be low the rate of vegetative spread is high. Professor F. W. Oliver (Carey and Oliver, 1918, p. 101) has given data for the areas of two plants over a period of four years which show a radial increment of from 0·33 to 1·3-metres per annum with an average increment of 0·7 m. The more rapidly growing individual, which at the outset occupied an area of 0·836 sq. metres, after an interval of four years occupied an area of 48·77 sq. m.

The facts given above are in conformity with the distribution of the Sea Convolvulus in Britain, for although, owing to vegetative spread, the species may be locally common it is in general rare, as we might expect from the low productivity and the fact that germination is probably dependent on suitable abrasion of the large (Av. weight, 0·0568 gm.) but hard-coated seeds.

## B. Species of Cultivated Ground and Similar Permanently Open Habitats

### Shepherd's-Purse (*Capsella species*)

The precocious self-fertilization of the members of this genus, before the flowers open, renders them comparable to apomictic species in the sense that every heritable variation tends to be perpetuated and, unless the mutation be deleterious, will multiply and not become obscured by intercrossing with other strains. As a consequence there are multitudes of different kinds of *Capsella* of varying status as regards the magnitude of their differences. The two types that have been studied are characterized as follows: The first, termed *Capsella simplex*, has radical leaves that are simple or but slightly lobed and bears fruits which are broadly triangular with slightly convex sides, whilst the upper edges of the two carpels are also noticeably convex. The aggregate that this typifies is perhaps rather more abundant in the early months of the year and on heavier soils than our second type, which is more frequent in the summer months and on lighter soils. The *C. heteris* group has pinnatisect radical leaves, of which the individual segments have an elongated distal lobe and a rounded adaxial lobe together, suggesting a closed hand with a pointing forefinger; the fruit is narrowly triangular with almost straight sides. In leaf form the two correspond to types distinguished by Shull, but I should hesitate to claim their identity and prefer to consider these as members of two aggregates sharing the features mentioned.

### *Capsella simplex*

One hundred specimens of this species were examined for fruit production, and the range observed was from seven to 679 capsules per plant. The average was $158{\cdot}3 \pm 9{\cdot}7$ fruits per plant ($\sigma$ 145; S.E.M. 14·5). The number of seeds per capsule in 74 capsules ranged from 11 to 34, with 77 per cent of the fruits containing between 20 and 30 seeds. The average was $23{\cdot}6 \pm 0{\cdot}4$

seeds per capsule, with a standard deviation of 5·2 and a standard error of the mean of 0·6. The average seed output is therefore 3,739±292, or approximately between 3,400 and 4,000 seeds per plant. The average germination is about 85 per cent, which implies a reproductive capacity of approximately three thousand two hundred.

*Capsella heteris*

The average number of fruits per plant for this species is slightly less than for its congener. The average observed was 142±16·7, with a range of from 12 to 357 fruits per plant. Here again the seeds were counted in 74 capsules, and the number varied between 3 and 31, but about 59 per cent of the fruits contained under ten seeds. The average number of seeds was 12·33±0·6 ($\sigma$ 7·9; S.E.M. 0·91). The mean seed output was therefore 1,819±232, or approximately between 1,500 and 2,000 seeds.

Nipplewort, *Lapsana communis* L.

This weed of cultivated ground is of interest in comparison with other Compositae which possess a pappus since its fruits have no such means of dispersal. The number of capitula per plant were counted on one hundred and twenty-two specimens and varied from seven to 585, as shown in Table LVIII.

The number of achenes per capitulum varied from 2 to 21, as follows: 2 (1), 3 (0), 4 (1), 5 (0), 6 (1), 7 (0), 8 (2), 9 (5), 10 (5), 11 (10), 12 (18), 13 (15), 14 (12), 15 (6), 16 (13), 17 (9), 18 (12), 19 (6), 20 (3), 21 (1).

TABLE LVIII. VARIATION IN NUMBER OF CAPITULA PER PLANT OF *LAPSANA COMMUNIS* L.

| Number of capitula | Number of plants | Number of capitula | Number of plants | Number of capitula | Number of plants | Number of capitula | Number of plants |
|---|---|---|---|---|---|---|---|
| 7 | 1 | 32 | 1 | 54 | 1 | 98 | 2 |
| 8 | 1 | 33 | 3 | 56 | 1 | 99 | 1 |
| 11 | 2 | 34 | 2 | 59 | 1 | 103 | 1 |
| 12 | 3 | 35 | 2 | 61 | 1 | 104 | 1 |
| 13 | 5 | 36 | 2 | 62 | 1 | 118 | 1 |
| 15 | 5 | 37 | 1 | 67 | 1 | 128 | 1 |
| 16 | 1 | 38 | 3 | 68 | 1 | 130 | 1 |
| 17 | 4 | 39 | 2 | 72 | 1 | 143 | 1 |
| 19 | 4 | 41 | 1 | 75 | 1 | 145 | 1 |
| 20 | 1 | 42 | 2 | 78 | 2 | 154 | 2 |
| 21 | 4 | 44 | 3 | 80 | 2 | 164 | 1 |
| 22 | 2 | 45 | 2 | 81 | 1 | 170 | 1 |
| 23 | 1 | 46 | 1 | 85 | 3 | 171 | 1 |
| 26 | 5 | 47 | 2 | 88 | 1 | 211 | 1 |
| 27 | 1 | 48 | 1 | 89 | 1 | 259 | 1 |
| 28 | 1 | 49 | 1 | 90 | 2 | 308 | 1 |
| 29 | 1 | 51 | 2 | 92 | 1 | 440 | 1 |
| 30 | 2 | 52 | 1 | 94 | 1 | 585 | 1 |
| 31 | 1 | 53 | 1 | 95 | 1 | | |

Total of 7,856 capitula on 122 plants.

The average number of achenes per capitulum for the 120 capitula was 14·44±0·2 ($\sigma$ 3·4; S.E.M. 0·3). The average number of capitula per plant was 64 (64·4)±5 ($\sigma$ 82·5; S.E.M. 7·5). The average output is therefore 930±85 per plant, or roughly between 850 and 1,000 fruits per plant.

Thale Cress, *Sisymbrium Thalianum* (L.) Gay

A total of 144 specimens of this weed were examined for fruit production and yielded 7,218 siliquas, distributed as shown in Table LIX.

TABLE LIX. VARIATION IN FRUIT PRODUCTION BY *SISYMBRIUM THALIANA* Hook.

| Number of siliquas | Number of individuals | Number of siliquas | Number of individuals | Number of siliquas | Number of individuals | Number of siliquas | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 23 | 1 | 48 | 3 | 89 | 1 |
| 3 | 2 | 25 | 2 | 50 | 1 | 90 | 2 |
| 4 | 2 | 26 | 1 | 54 | 3 | 103 | 2 |
| 5 | 3 | 27 | 2 | 55 | 3 | 105 | 1 |
| 6 | 1 | 28 | 4 | 56 | 4 | 106 | 1 |
| 7 | 1 | 29 | 0 | 57 | 2 | 115 | 1 |
| 8 | 2 | 30 | 1 | 58 | 2 | 118 | 2 |
| 9 | 5 | 31 | 2 | 60 | 1 | 120 | 1 |
| 10 | 3 | 32 | 2 | 61 | 1 | 123 | 1 |
| 11 | 6 | 33 | 1 | 63 | 1 | 124 | 1 |
| 12 | 3 | 34 | 1 | 64 | 2 | 125 | 1 |
| 13 | 3 | 39 | 2 | 65 | 1 | 131 | 1 |
| 14 | 1 | 40 | 2 | 66 | 1 | 133 | 1 |
| 15 | 6 | 41 | 1 | 71 | 1 | 147 | 1 |
| 16 | 5 | 42 | 1 | 72 | 1 | 174 | 1 |
| 17 | 1 | 43 | 1 | 75 | 1 | 190 | 1 |
| 18 | 2 | 44 | 1 | 77 | 1 | 203 | 1 |
| 19 | 1 | 45 | 3 | 80 | 2 | 253 | 1 |
| 21 | 4 | 46 | 2 | 82 | 1 | 478 | 1 |
| 22 | 5 | 47 | 2 | 85 | 1 | | |

Total of 7,218 siliquas on 144 plants.

The average number of siliquas per plant was 50±3·1 ($\sigma$ 56·1; S.E.M. 4·67). The number of seeds was counted in sixteen fruits and ranged from 18 to 45, with an average of 33·4±1·1 ($\sigma$ 6·8; S.E.M. 1·7). The mean seed output is therefore approximately between 1,500 and 1,800 seeds per plant. This represents an average weight of seed of from 0·046 gm. to 0·055 gm. per plant.

Sow Thistle, *Sonchus oleraceus* L.

Sixty-five plants showed a range in number of fruiting capitula of from 6 to two hundred and eighty-nine. The total number was 2,842, or an average of 43·7±3·8 ($\sigma$ 46·7; S.E.M. 5·8) fruiting capitula per plant. Sixteen fruiting capitula yielded a total of 2,246 fruits, the number per capitulum ranging from 96 to 200 fruits. The average was 140±4·9 fruits per capitulum ($\sigma$ 29·2; S.E.M. 7·3).

The average fruit production per plant would therefore be 6,136±746, or, in round figures, between 5,400 and 6,900 fruits per plant. The average weight of achenes per plant would be about 2·677 gm. N. T. Gill (1938) records 100 per cent germination for this species.

Two types of this species occur, namely a diploid with sixteen chromosomes in the somatic cells (Marchal, 1920) and a tetraploid with thirty-two. It is of interest to note that the latter, as recently pointed out by H. N. Barber (1941), is apparently the more widespread.

Prickly Sow Thistle, *Sonchus asper* Hoffm.

Only twenty-five plants of this species were studied, and showed a range of from 13 to 304 fruiting capitula per plant and a total of two thousand six hundred and twenty-three. The average was thus 105±10 ($\sigma$ 75·5; S.E.M. 15). The number of achenes were counted in sixteen capitula, and totalled 3,160 or an average of 197·5±6·2 ($\sigma$ 37·2; S.E.M. 9·3). These data suggest a fruit production averaging about 23,000±2,627). In view of the small number of specimens examined no great importance can be attached to this figure, but it would appear that the production of fruits is appreciably greater than for *S. oleraceus*.

The largest specimen of the latter species would have yielded about 40,000 fruits as compared with 600,000 for the largest specimen of *Sonchus asper*.

Attention may be called to the fact that both these species have much larger average seed outputs than *Lapsana communis*, although the efficiency of their fruit dispersal is far greater owing to the absence of a pappus from the fruits of *Lapsana*.

Creeping Sow Thistle, *Sonchus arvensis* L.

Unlike the two preceding species which are either annual or biennial, this is a perennial which spreads rapidly by root shoots that renders delimitation of individuals difficult, and only eleven plants, sufficiently isolated, were found on which to count the fruiting heads. These ranged in number from 28 to 131 with an average of 85±6·4.

The number of fruits in each capitulum ranged from 105 to 191, with an average of 156±59. Thus the average number of fertile fruits per plant was 13,297±1,500. Actually this may well be an underestimate, since older plants are usually those which cannot be delimited. It is worthy of note that in spite of the copious vegetative propagation the seed output, even on these data, considerably exceeds those of its annual congeners. Kempski, however, records only a 5 per cent germination for this species.

Penny Cress, *Thlaspi arvense* L.

Fifty-eight specimens of this species were examined for fruit production. The number of siliculas totalled 10,247, and for the individual plants ranged from 46 to seven hundred and eighty. The average number of fruits was 177 (176·7±12·7; $\sigma$ 145·8; S.E.M. 19·1). The number of seeds was determined in seventy-two fruits and varied as shown in Table LX.

TABLE LX. VARIATION IN NUMBER OF SEEDS PER FRUIT OF *THLASPI ARVENSE*

| Number of seeds | Number of fruits | Number of seeds | Number of fruits |
|---|---|---|---|
| 3 | 1 | 11 | 10 |
| 5 | 1 | 12 | 8 |
| 7 | 2 | 13 | 11 |
| 8 | 6 | 14 | 4 |
| 9 | 9 | 15 | 6 |
| 10 | 13 | 16 | 1 |

Average 11·0±0·19 ($\sigma$ 2·48; S.E.M. 0.29) seeds per fruit.

The average seed output is thus 1,948±174 or about 1,800 to 2,100 seeds per plant. Stevens obtained 562 specimens during two seasons which yielded 263,400 seeds, or an average of 468 per plant, which is about one-quarter of our average.

## Venus's Looking-Glass, *Specularia hybrida* DC. (*Legousia*)

A total of one hundred and sixty-nine plants were examined for fruit production, and these showed in a striking manner the feature, to which attention has already been drawn, which characterizes many annual species, namely the occurrence of a high proportion of small individuals and a small number of large ones.

TABLE LXI*a*. VARIATION IN CAPSULE NUMBER PER PLANT OF *SPECULARIA HYBRIDA* DC.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|
| 1 | 20 | 10 | 5 |
| 2 | 18 | 11 | 5 |
| 3 | 35 | 12 | 2 |
| 4 | 19 | 13 | 1 |
| 5 | 8 | 14 | 2 |
| 6 | 6 | 16 | 2 |
| 7 | 6 | 19 | 3 |
| 8 | 5 | 20 | 2 |
| 9 | 5 | 24 | 1 |

Also 25 (1), 29 (2), 33 (1), 34 (1), 35 (1), 38 (1), 42 (1), 43 (1), 44 (2), 45 (1), 46 (1), 48 (1), 50 (1), 54 (1), 58 (2), 63 (1), 84 (1), 101 (1), 115 (1), 128 (1), 252 (1).

Average 13·3±1·39 fruits per plant ($\sigma$ 27·1; S.E.M. 2·08).

Plants with twelve capsules or fewer represent nearly 80 per cent of the total population examined, but their productivity of seeds was only about one-quarter of the whole. In other words, about 75 per cent of the seeds produced were the harvest of the small number of unusually large plants. The seed crop in this, as in many other species, is therefore in no small degree dependent upon the proportion of large plants rather than on the number of individuals.

The seeds were counted in fifty-one capsules and ranged in number from

8 to 81, as shown in Table LXI*b*. The average is 40 seeds per capsule ($40 \cdot 3 \pm 1 \cdot 6$; $\sigma$ 16·8; S.E.M. 2·4).

TABLE LXI*b*. VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *SPECULARIA HYBRIDA* DC.

| Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules |
|---|---|---|---|---|---|---|---|
| 8 | 1 | 26 | 1 | 43 | 4 | 57 | 1 |
| 11 | 1 | 27 | 1 | 44 | 1 | 58 | 1 |
| 12 | 1 | 28 | 2 | 45 | 2 | 59 | 1 |
| 16 | 2 | 30 | 1 | 46 | 2 | 60 | 2 |
| 17 | 1 | 31 | 2 | 47 | 1 | 61 | 2 |
| 21 | 1 | 33 | 1 | 49 | 1 | 65 | 1 |
| 23 | 2 | 36 | 2 | 50 | 1 | 70 | 2 |
| 24 | 1 | 37 | 2 | 51 | 2 | 81 | 1 |
| 25 | 1 | 39 | 2 | 53 | 1 | | |

Total of 2,055 seeds in 51 capsules.

The mean seed output is therefore $538 \pm 77$ seeds per plant, or roughly between five and six hundred seeds per plant.

Ivy-leaved Speedwell, *Veronica hederaefolia* L.

The fruits were counted on 121 plants of this species and totalled one thousand nine hundred and forty-five. The number per plant varied from 2 to 65, and the average was $16 \cdot 07 \pm 0 \cdot 99$. The standard deviation was 11·53 and the standard error of the mean 1·48.

TABLE LXII. VARIATION IN NUMBER OF FRUITS PER PLANT OF *VERONICA HEDERAEFOLIA* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 2 | 2 | 12 | 3 | 22 | 4 | 33 | 1 |
| 3 | 5 | 13 | 8 | 23 | 2 | 34 | 1 |
| 4 | 3 | 14 | 4 | 24 | 3 | 46 | 1 |
| 5 | 6 | 15 | 5 | 25 | 2 | 48 | 1 |
| 6 | 11 | 16 | 5 | 26 | 3 | 50 | 1 |
| 7 | 4 | 17 | 2 | 27 | 3 | 64 | 1 |
| 8 | 4 | 18 | 6 | 28 | 3 | 65 | 1 |
| 9 | 5 | 19 | 1 | 29 | 4 | | |
| 10 | 5 | 20 | 3 | 30 | 1 | | |
| 11 | 3 | 21 | 3 | 32 | 1 | | |

Total of 1,945 capsules on 121 plants.

The seeds were counted in 50 capsules and ranged from one to four, with two seeds as the mode [1 seed (11 capsules), 2 (16), 3 (12), 4 (10)]. The mean number is therefore $2 \cdot 4 \pm 0 \cdot 1$ ($\sigma$ 1·10; S.E.M. 0·157). The mean seed output is therefore from 35 to 43 seeds per plant ($38 \cdot 66 \pm 3 \cdot 98$).

*Silene quinquevulnera* L. (*S. gallica* v. *quinquevulnera*)

The number of capsules produced by plants of *Silene quinquevulnera* was determined as shown in Table LXIII for 289 plants, and ranged from one to

TABLE LXIII. VARIATION IN FRUIT PRODUCTION BY *SILENE QUINQUEVULNERA* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 27 | 16 | 7 | 33 | 1 | 63 | 2 |
| 2 | 25 | 17 | 8 | 35 | 2 | 75 | 1 |
| 3 | 31 | 18 | 8 | 36 | 1 | 91 | 1 |
| 4 | 33 | 19 | 1 | 37 | 1 | 98 | 1 |
| 5 | 18 | 20 | 3 | 38 | 1 | 115 | 1 |
| 6 | 12 | 21 | 0 | 39 | 2 | 116 | 1 |
| 7 | 6 | 22 | 2 | 41 | 1 | 123 | 1 |
| 8 | 14 | 23 | 1 | 44 | 1 | 136 | 1 |
| 9 | 8 | 24 | 3 | 45 | 1 | 163 | 1 |
| 10 | 7 | 25 | 1 | 50 | 1 | 194 | 1 |
| 11 | 11 | 26 | 2 | 51 | 1 | 204 | 1 |
| 12 | 5 | 28 | 1 | 53 | 1 | 265 | 1 |
| 13 | 8 | 29 | 1 | 54 | 1 | 327 | 1 |
| 14 | 6 | 31 | 1 | 56 | 1 | 479 | 1 |
| 15 | 4 | 32 | 1 | 60 | 2 | | |

Total for 289 plants of 5,365 capsules. Average 18 (18·39$\pm$1·7) capsules per plant.

four hundred and seventy-nine. The mode would appear to be three or four capsules, but the average for all the specimens was 18·39$\pm$1·7 ($\sigma$ 44·4; S.E.M. 2·61). The variation in number of seeds per capsule is shown in Table LXIV,

TABLE LXIV. VARIATION IN NUMBER OF SEEDS IN CAPSULES OF *SILENE QUINQUEVULNERA* L.

| Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules |
|---|---|---|---|---|---|---|---|
| 19 | 2 | 39 | 4 | 52 | 4 | 64 | 4 |
| 24 | 2 | 40 | 3 | 53 | 2 | 65 | 2 |
| 28 | 1 | 41 | 2 | 54 | 1 | 66 | 2 |
| 29 | 1 | 42 | 3 | 55 | 5 | 67 | 1 |
| 30 | 2 | 43 | 2 | 56 | 2 | 69 | 2 |
| 32 | 3 | 44 | 2 | 57 | 2 | 72 | 1 |
| 33 | 1 | 46 | 6 | 58 | 2 | 73 | 2 |
| 34 | 3 | 47 | 2 | 59 | 1 | 78 | 1 |
| 35 | 1 | 48 | 2 | 60 | 4 | 80 | 1 |
| 36 | 1 | 49 | 2 | 61 | 2 | | |
| 37 | 1 | 50 | 1 | 62 | 5 | | |
| 38 | 3 | 51 | 2 | 63 | 6 | | |

Total of 5,217 seeds in 104 capsules. Average 50·1$\pm$0·9.

and exhibits a range from 19 to 80 seeds, with an average of 50·1$\pm$0·9 ($\sigma$ 13·3; S.E.M. 1·3). From these data the average seed output is 923$\pm$102 seeds per plant, or approximately between eight hundred and a thousand. The

average germination is 80 per cent, so that the average reproductive capacity is 738±81·6.

Sandwort, *Arenaria serpyllifolia* L.

Thirty-one plants of this species produced fruits ranging in number from as few as six to one thousand and forty-four. The average was 208±27·4 capsules per plant ($\sigma$ 229; S.E.M. 41·6).

The number of seeds was counted in eighty capsules and showed a range in number as follows:

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|
| 10 | 1 | 17 | 15 |
| 11 | 3 | 18 | 17 |
| 12 | 4 | 19 | 6 |
| 13 | 2 | 20 | 7 |
| 14 | 2 | 21 | 9 |
| 15 | 6 | 22 | 2 |
| 16 | 6 | | |

The total number of seeds in the eighty capsules was 1,379, an average of 17·2±0·2 seeds per capsule ($\sigma$ 2·8; S.E.M. 0·3). The average seed output is therefore 3,583±513 seeds per plant.

*Arenaria tenuifolia* L.

Forty-eight plants of this species produced the following number of capsules: 10 (1), 19 (2), 20 (1), 21 (2), 24 (5), 25 (1), 26 (1), 28 (2), 33 (1), 36 (1), 37 (1), 45 (1), 46 (1), 48 (1), 50 (1), 53 (1), 55 (1), 56 (1), 63 (1), 67 (1), 72 (1), 77 (2), 82 (1), 85 (1), 91 (1), 92 (1), 93 (2), 100 (1), 108 (1), 109 (1), 111 (1), 119 (1), 124 (1), 137 (1), 143 (1), 147 (1), 188 (1), 191 (1), 217 (1). A total of 3,332 capsules, or an average of 69·4±4·82 capsules per plant ($\sigma$ 49·9; S.E.M. 7·23).

The seeds in eighteen capsules varied as follows: 13 (1), 14 (1), 16 (1), 17 (1), 18 (1), 19 (2), 21 (1), 22 (2), 23 (2), 26 (2), 29 (1), 30 (1), 34 (1), 35 (1). A total of 406 seeds, or an average of 22·55±1·0 seeds per capsule ($\sigma$ 6·4; S.E.M. 1·5). The average seed output is therefore 1,569±178 seeds per plant, and the average reproductive capacity is 1,368±153 potential offspring per plant (average germination 86·2 per cent).

Corn-Cockle, *Lychnis* (*Agrostemma*) *Githago* (L.) Scop.

The capsules on 141 plants varied as shown in Table LXV. They ranged in number from two fruits to forty-seven, with an average of 12·7±0·5, a figure which corresponds closely with the mode, viz. eleven. An unusual occurrence; but even here it will be noted that there is almost as great a frequency of plants with two capsules, and nearly 19 per cent of the specimens examined developed over twenty capsules. The standard deviation is 8·8 and the S.E.M. 0·74.

The number of seeds in the individual capsules ranged from six to 42, with a mode in the region of twenty-eight. The average number of seeds was 25 (24·7±0·43; $\sigma$ 8·24; S.E.M. 0·65).

TABLE LXV. VARIATION IN NUMBER OF CAPSULES PER PLANT OF *LYCHNIS GITHAGO* (L.) SCOP.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 10 | 3 | 19 | 5 | 29 | 1 |
| 2 | 12 | 11 | 13 | 20 | 3 | 33 | 1 |
| 3 | 4 | 12 | 6 | 21 | 3 | 34 | 3 |
| 4 | 6 | 13 | 5 | 22 | 4 | 35 | 1 |
| 5 | 8 | 14 | 7 | 23 | 2 | 41 | 1 |
| 6 | 7 | 15 | 5 | 24 | 4 | 47 | 1 |
| 7 | 4 | 16 | 3 | 25 | 1 | | |
| 8 | 9 | 17 | 5 | 26 | 2 | | |
| 9 | 5 | 18 | 3 | 27 | 2 | | |

Total of 1,802 capsules on 141 plants.

TABLE LXVI.—VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *LYCHNIS GITHAGO* (L.) SCOP.

| Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules |
|---|---|---|---|---|---|---|---|
| 6 | 1 | 16 | 3 | 26 | 5 | 36 | 4 |
| 7 | 1 | 17 | 8 | 27 | 6 | 37 | 1 |
| 8 | 3 | 18 | 9 | 28 | 12 | 38 | 3 |
| 9 | 0 | 19 | 4 | 29 | 10 | 39 | 2 |
| 10 | 4 | 20 | 2 | 30 | 11 | 40 | 0 |
| 11 | 2 | 21 | 6 | 31 | 5 | 41 | 1 |
| 12 | 2 | 22 | 5 | 32 | 4 | 42 | 1 |
| 13 | 2 | 23 | 5 | 33 | 9 | | |
| 14 | 7 | 24 | 1 | 34 | 7 | | |
| 15 | 5 | 25 | 6 | 35 | 4 | | |

Total of 3,917 seeds in 161 capsules. Average $24{\cdot}7 \pm 0{\cdot}43$ seeds per capsule.

The average number of seeds per plant is thus $314 \pm 18$, or a seed output of between 296 and three hundred and thirty-two. The largest plant would have produced about 3,150 seeds, which is appreciably higher than Nobbe's estimate for this species of up to 2,592 seeds. Perseke's estimate of 1,000–2,000 seeds per plant is clearly too high and doubtless ignored the considerable proportion of small individuals in a normal population. The average germination is about 68 per cent, so that the average reproductive capacity would be $231{\cdot}5 \pm 12{\cdot}2$, or approximately between 220 and 240 offspring per plant.

The seeds of *L. Githago* are exceptionally large (*ca.* 3·5 mm.) for a species of open habitats and contain a poisonous glucoside. The seeds of the Darnel Grass (*Lolium temulentum*) contain a narcotic alkaloid, and this plant too was sometimes called Corn-cockle and was formerly a common cornfield weed, though now rare. Shakespeare's contemporary, Drayton, referred to the "crimson Darnel-flower," but, although the confusion of popular nomenclature calls for caution, it is obvious that, despite the large size of the seeds, *L. Githago* was at one time a widespread pest.

Scarlet Pimpernel, *Anagallis arvensis* L.

We have already given data respecting the number of seeds in capsules of this species. The average for 3,105 capsules was found to be 17·86±0·07. The number of capsules per plant was determined for 135 plants, and varied from a single capsule to 236 capsules. The average number of capsules was 50·44±2·9 per plant ($\sigma$ 50·3; S.E.M. 4·3). The average seed output is therefore 902±54 seeds per plant.

Blue Pimpernel, *Anagallis foemina* Mill.

The number of fruits of this species was determined for eighty-six plants. The range of variation as shown in Table LXVII was from one capsule to five hundred and seventy. The average number of capsules was 33·0±4·9 ($\sigma$ 68·6; S.E.M. 7·3). The number of seeds was counted in a total of 162 capsules, and varied from four to twenty-four, with an average of 14·1±0·22 seeds per capsule ($\sigma$ 4·2; S.E.M. 0·33). The average seed output would therefore be 466±76 seeds per plant, or about half that of *A. arvensis*. The reproductive capacities of the two species probably show a greater difference, as,

TABLE LXVII. VARIATION IN NUMBER OF CAPSULES OF *ANAGALLIS FOEMINA* MILL.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 15 | 5 | 28 | 4 | 47 | 1 |
| 3 | 1 | 16 | 4 | 29 | 1 | 55 | 1 |
| 4 | 4 | 17 | 2 | 30 | 2 | 57 | 1 |
| 6 | 5 | 18 | 1 | 31 | 2 | 60 | 1 |
| 7 | 2 | 19 | 2 | 32 | 1 | 72 | 1 |
| 8 | 4 | 20 | 2 | 34 | 1 | 84 | 1 |
| 9 | 3 | 21 | 1 | 38 | 3 | 214 | 1 |
| 10 | 1 | 22 | 1 | 39 | 1 | 261 | 1 |
| 11 | 2 | 23 | 2 | 40 | 1 | 570 | 1 |
| 12 | 5 | 24 | 1 | 41 | 2 | | |
| 14 | 2 | 26 | 5 | 43 | 1 | | |

Total of 2,838 capsules on 86 plants. Average 33±4·9.

TABLE LXVIII. VARIATION IN SEED NUMBER IN CAPSULES OF *ANAGALLIS FOEMINA* MILL.

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|---|---|---|---|
| 4 | 2 | 10 | 13 | 16 | 13 | 22 | 3 |
| 5 | 2 | 11 | 7 | 17 | 13 | 23 | 1 |
| 6 | 3 | 12 | 10 | 18 | 16 | 24 | 1 |
| 7 | 4 | 13 | 6 | 19 | 4 | | |
| 8 | 5 | 14 | 20 | 20 | 4 | | |
| 9 | 9 | 15 | 18 | 21 | 8 | | |

Total of 2,284 seeds in 162 capsules. Average 14·1±0·22.

though exact data are not available, the germination of *A. foemina* has probably a lower average percentage value than for *A. arvensis*. Furthermore, in wet seasons the proportion of viable seeds is very low, a feature which is reflected in the very marked changes of population which this species exhibits in localities where it is permanently established. The relative frequencies of these two Pimpernels is thus probably in accord with their respective reproductive capacities.

*Claytonia perfoliata* Don.

This introduction from North America, first recorded in 1852, is now abundant on the sandy heaths of Breckland, Surrey, and elsewhere. The fruits were counted on a random selection of only twenty-one plants, and ranged in number from 15 to three hundred and sixty-three. The average number was $153 \pm 13$. All the fruits examined contained three seeds, so that the average seed output would be $459 \pm 39$. The shining black seeds weigh 0·00079 gm. and germinate from September to October. The plant is therefore a winter annual.

Groundsel, *Senecio vulgaris* L.

The Common Groundsel occurs in a few natural habitats, such as dunes and shingle beaches, but the four hundred and forty-eight plants, for which the number of capitula are here enumerated, were obtained from waste ground. Professor Trow showed that the Linnean aggregate comprises a

TABLE LXIX. VARIATION IN NUMBER OF CAPITULA OF *SENECIO VULGARIS* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 9 | 22 | 10 | 43 | 3 | 68 | 1 |
| 2 | 16 | 23 | 11 | 44 | 5 | 75 | 1 |
| 3 | 26 | 24 | 7 | 45 | 4 | 76 | 1 |
| 4 | 19 | 25 | 5 | 46 | 3 | 77 | 1 |
| 5 | 20 | 26 | 4 | 47 | 2 | 80 | 1 |
| 6 | 13 | 27 | 6 | 48 | 2 | 88 | 3 |
| 7 | 17 | 28 | 6 | 49 | 2 | 94 | 1 |
| 8 | 19 | 29 | 7 | 50 | 4 | 96 | 1 |
| 9 | 6 | 30 | 5 | 51 | 3 | 97 | 1 |
| 10 | 12 | 31 | 6 | 52 | 1 | 103 | 1 |
| 11 | 20 | 32 | 3 | 54 | 3 | 104 | 1 |
| 12 | 4 | 33 | 6 | 55 | 2 | 122 | 1 |
| 13 | 8 | 34 | 4 | 57 | 2 | 124 | 1 |
| 14 | 9 | 35 | 5 | 58 | 5 | 128 | 1 |
| 15 | 15 | 36 | 5 | 60 | 1 | 140 | 1 |
| 16 | 14 | 37 | 2 | 61 | 2 | 141 | 1 |
| 17 | 11 | 38 | 2 | 62 | 1 | 237 | 1 |
| 18 | 11 | 39 | 3 | 63 | 2 | 283 | 1 |
| 19 | 8 | 40 | 1 | 64 | 2 | 407 | 1 |
| 20 | 2 | 41 | 4 | 65 | 3 | | |
| 21 | 11 | 42 | 1 | 67 | 2 | | |

**Total of 11,078 capitula on 448 plants. Average 25 (24·7).**

number of microspecies, but the material here dealt with was carefully examined, and all the specimens appeared to belong to the same microspecies. It will be noted that more than a quarter of the individuals bear from one to seven capitula only, whilst the eighty plants bearing forty or more capitula produce as many as the remaining 82 per cent of the entrie population. The average number of capitula per plant is $24{\cdot}7 \pm 1$ ($\sigma$ 33; S.E.M. 1·57).

The achenes were counted in a random sample of sixty-eight fruiting heads and ranged in number from 22 to 68, distributed as follows: 22 (1), 25 (2), 26 (1), 28 (1), 30 (1), 31 (2), 32 (1), 34 (1), 35 (2), 36 (3), 38 (3), 39 (1), 40 (5), 42 (2), 43 (4), 44 (1), 45 (1), 46 (2), 47 (5), 48 (1), 49 (2), 50 (2), 51 (4), 52 (2), 53 (1), 54 (4), 55 (1), 56 (1), 57 (1), 58 (4), 62 (1), 65 (3), 66 (1), 68 (1). The average is $45{\cdot}6 \pm 0{\cdot}6$ fruits per capitulum ($\sigma$ 8·4; S.E.M. 1·0).

The average seed output is therefore $1{,}127 \pm 60$ per plant, and the reproductive capacity is probably over 1,000, as the percentage germination is usually about ninety.

Pineapple Weed, *Matricaria suaveolens* (Pursh) Buch. (*M. discoidea* DC.)

One hundred and eighty-four plants of this introduction from Oregon, which has spread with such remarkable rapidity since the development of motor transport in this country, were examined for production of capitula. These ranged in number from a single capitulum to 467 capitula per plant. The total number of capitula was 6,955, or an average of $43 \pm 3{\cdot}1$ ($\sigma$ 64; S.E.M. 4·7).

The number of achenes produced in each capitulum ranged from 55 to 458, and for twenty-five capitula totalled three thousand six hundred and ninety-two. The average was $147{\cdot}68 \pm 11{\cdot}5$ ($\sigma$ 86·7; S.E.M. 17·3). The average output is thus $6{,}384 \pm 350$ per plant. Germination tests indicated a high rate of germination of about 93 per cent, so that the reproductive capacity would be $5{,}937 \pm 325$.

*Cerastium glomeratum* Thuillier (*C. viscosum* L.)

Forty-one plants of this species were examined for fruit production, which ranged from 11 to 634 per plant. The average was $91 \pm 11{\cdot}3$ ($\sigma$ 109·1; S.E.M. 17). The seeds were counted in thirteen capsules and varied from 41 to 62, with an average of $51{\cdot}8 \pm 1{\cdot}08$ ($\sigma$ 5·85; S.E.M. 1·62).

The average seed output would therefore appear to be about $4{,}725 \pm 685$ seeds per plant. This represents an average weight of seed of approximately 0·225 gm. per plant. In its natural habitats, shallow soils, dry sandy heaths, and dunes, the seed output would be appreciably lower.

Thorow-wax, *Bupleurum rotundifolium* L.

Although only five plants of this species were available for examination they included one very large specimen, one small plant, and three that were probably about average-sized individuals. The respective numbers of schizachenes produced were as follows: 70, 204, 252, 360, and 880, an average of 353 per plant ($353 \pm 83$; $\sigma$ 279; S.E.M. 125). The species is a weed of calcareous cornfields, southern-continental in its distribution, which may

well account for the low germination usually shown by seed ripened in this country. These suggest that the average germination may not exceed 15 per cent, which on the above figures would represent an average reproductive capacity of not more than about 53 potential offspring per plant. Even if these figures be too low it is quite manifest that the rarity of the species in England may well be related to its low reproduction rate. As the species is a summer annual, germination taking place in April, the cause of its rarity cannot be attributed to winter condition.

TABLE LXX. SUMMARY OF DATA OF SEED OUTPUT OF SPECIES OF PERMANENTLY OPEN HABITATS

| Species | Average seed output | Average reproductive capacity |
|---|---|---|
| Veronica hederaefolia | 39±4 | |
| Cardamine hirsuta (dune plants) | 98 | |
| Erophila praecox | 135±12 | |
| Hypochoeris glabra | 138±16 | 130 |
| Medicago minima | 150±32 | 67 |
| Cerastium semidecandrum | 256±28 | ? *ca.* 140 |
| Statice binervosa | 300 | |
| Lychnis Githago | 314±18 | 213 |
| Bupleurum rotundifolium | 353±83 | ? *ca.* 50 |
| Hutchinsea petraea | 396±42 | ? *ca.* 50 |
| Claytonia perfoliata | 459±39 | |
| Anagallis foemina | 466±76 | |
| Erophila Boerhavii | 557±52 | |
| Cardamine hirsuta (cultivated ground) | 640 | ? *ca.* 600 |
| Silene anglica | 716 | 573 |
| Silene conica | 784±84 | 768 |
| Specularia hybrida | 829±222 | |
| Anagallis arvensis | 902±54 | |
| Silene quinquevulnera | 923±102 | 738 |
| Lapsana communis | 930±85 | |
| Saxifraga tridactylites | 1,106±98 | ? 774 |
| Senecio vulgaris | 1,127±60 | >1,000 |
| Solanum nigrum | 1,448 | ? 1,400 |
| Arenaria tenuifolia | 1,569±178 | 1,368 |
| Sisymbrium Thaliana | 1,650±150 | |
| Papaver hybridum | 1,674±208 | 1,529 |
| Capsella heteris | 1,819±232 | |
| Thlaspi arvense | 1,948±174 | ? *ca.* 1,000 |
| Papaver argemone | 1,998±228 | 1,258 |
| Linaria minor | 2,168±320 | ? 867 |
| Arenaria serpyllifolia | 3,583±513 | ? 3,500 |
| Capsella simplex | 3,739±292 | 3,200 |
| Cerastium glomeratum | 4,725±685 | |
| Erodium moschatum | 5,445±442 | *ca.* 5,000 |
| Sonchus oleraceus | 6,136±746 | |
| Hyoscyamus niger | 6,278±522 | |
| Matricaria suaveolens | 6,384±350 | 5,937 |
| Papaver dubium | 13,777±1,563 | 5,757 |
| Papaver Rhoeas | 17,070±2,374 | 10,928 |
| Sonchus asper | 23,138±1,713 | |

Arithmetic mean of averages for thirty-nine species 2,904 seeds per plant.

We may for convenience summarize the data for species of permanently open habitats, placing these in the order of increasing magnitude.

Attention may be drawn to the fact that though the average is about 2,900 seeds per plant, yet of all the species only one-quarter have an output which exceeds this figure, whilst half have average seed outputs of under one thousand. Thus, although some species of waste ground have large, and sometimes even very large, productiveness the general rule amongst species of permanently open habitats would appear to be a rather low output of seed.

Adequate germination data are only available for a few of the species concerned, so that the reproductive capacities in a large proportion either cannot be given or only roughly assessed. But these data are sufficient to show that a low percentage germination cannot be said to be normally compensated by a large seed production; seed output and reproductive capacity tend, in fact, to increase together. The absence of such a negative correlation is in itself evidence that the magnitude of the seed output is not mainly determined by mortality risks, since a low percentage germination is but an index of high mortality in the early stages of embryo formation or development.

## Species of Semi-open Habitats

Several of the species of which data have already been furnished belong to this category. These include *Gentiana axillaris*, *G. praecox*, *G. Germanica*, and *Erythraea umbellata*. Such, in common with those about to be considered, are features of the short turf of chalk downs and colonize where the vegetation is comparatively open. Such species also occur where the habitat is completely open but clearly differ from the species of permanently open habitats in tolerating a slight measure of competition.

Flea-bane, *Erigeron acre* L.

Individuals of this species, both from calcareous habitats and from sandy soils, were studied. The fruiting capitula were counted on 161 individuals and showed the range portrayed in Table LXXI. From this it will be seen that

TABLE LXXI. VARIATION IN NUMBER OF FRUITING CAPITULA PER PLANT OF *ERIGERON ACRE* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 11 | 5 | 22 | 4 | 50 | 1 |
| 2 | 1 | 12 | 11 | 25 | 3 | 58 | 1 |
| 3 | 7 | 13 | 7 | 26 | 1 | 59 | 1 |
| 4 | 13 | 14 | 6 | 27 | 1 | 65 | 1 |
| 5 | 7 | 15 | 4 | 28 | 1 | 68 | 1 |
| 6 | 19 | 16 | 1 | 31 | 1 | 88 | 1 |
| 7 | 15 | 17 | 1 | 32 | 1 | 136 | 1 |
| 8 | 18 | 18 | 3 | 33 | 2 | 209 | 1 |
| 9 | 6 | 20 | 3 | 34 | 1 | 277 | 1 |
| 10 | 6 | 21 | 2 | 36 | 1 | | |

**Total of 2,652 capitula on 161 plants.**

although the average number of fruiting capitula is sixteen (16·4±0·8; $\sigma$ 30·2; S.E.M. 2·3) the mode is from six to eight capitula per plant, whilst the proportion of individuals bearing from four to eight fruiting capitula was 44 per cent. The fruits in a capitulum were counted in twenty-one examples, as follows: 46, 74, 88, 108, 109, 111, 112, 124, 133, 136, 139, 141, 148, 150, 155, 157 (three capitula), 163, 166, 167; a total of 2,745 fruits, or an average of 130·7±4·7 ($\sigma$ 31·7; S.E.M. 7·0). Thus the average seed output would be 2,147±182, or between 1,965 and 2,329 per plant. It may be well to point out that if an attempt had been made to estimate the seed output by selection of an " average " individual and an " average " capitulum as judged by eye, the probability is that the estimate would have been 7×*ca.* 150, or about half the real average.

Carline Thistle, *Carlina vulgaris* L.

This species is not only a feature of the short and more open turf of the chalk down but is also characteristic of the more calcareous dune systems. Specimens were examined from both types of habitat, namely 95 individuals from chalk downs and 110 from dune systems; but as the means and degree of dispersion were not significantly different the data are collectively considered in Table LXXII.

TABLE LXXII. VARIATION IN NUMBER OF CAPITULA PER PLANT OF *CARLINA VULGARIS* L.

| Number of fruiting capitula | Number of individuals | Number of fruiting capitula | Number of individuals |
|---|---|---|---|
| 1 | 15 | 12 | 3 |
| 2 | 43 | 13 | 1 |
| 3 | 62 | 14 | 0 |
| 4 | 34 | 15 | 4 |
| 5 | 12 | 16 | 2 |
| 6 | 10 | 17 | 0 |
| 7 | 2 | 18 | 0 |
| 8 | 4 | 19 | 0 |
| 9 | 3 | 20 | 2 |
| 10 | 5 | 21 | 2 |
| 11 | 1 | | |

Total of 900 fruiting capitula on 205 plants.

An average of 4·4±0·17 capitula per plant ($\sigma$ 3·7; S.E.M. 0·26).

The number of fruits in the capitula examined ranged from 109 to 197, with an average of 154±10·1, so that the average seed output would be 679±71 per plant.

Purging Flax, *Linum catharticum* L.

Two hundred and fifty-two plants of this species were examined for fruit production, the number ranging from 3 to nine hundred and seventy-two. The distribution is shown in Table LXXIII.

The average number of fruits per plant is twenty-seven (27·3±2·7; $\sigma$ 65·9; S.E.M. 4·1). The number of seeds per capsule, except in depauperate plants, is almost always five, so that the average seed output is 136·5±13·5. The germination would appear to be somewhat variable, as Kinzel obtained only

TABLE LXXIII. VARIATION IN FRUIT PRODUCTION BY *LINUM CATHARTICUM* L.

| Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals |
|---|---|---|---|---|---|---|---|
| 3 | 5 | 19 | 6 | 35 | 1 | 60 | 1 |
| 4 | 3 | 20 | 9 | 36 | 2 | 64 | 1 |
| 5 | 15 | 21 | 3 | 37 | 2 | 65 | 1 |
| 6 | 13 | 22 | 4 | 38 | 2 | 67 | 1 |
| 7 | 12 | 23 | 3 | 39 | 2 | 72 | 2 |
| 8 | 7 | 24 | 6 | 40 | 3 | 73 | 2 |
| 9 | 12 | 25 | 4 | 45 | 2 | 74 | 2 |
| 10 | 9 | 26 | 9 | 46 | 1 | 75 | 1 |
| 11 | 10 | 27 | 3 | 47 | 3 | 78 | 1 |
| 12 | 11 | 28 | 2 | 48 | 1 | 82 | 1 |
| 13 | 6 | 29 | 1 | 50 | 1 | 155 | 1 |
| 14 | 8 | 30 | 1 | 51 | 1 | 158 | 1 |
| 15 | 12 | 31 | 3 | 52 | 2 | 206 | 1 |
| 16 | 14 | 32 | 5 | 53 | 1 | 267 | 1 |
| 17 | 3 | 33 | 1 | 55 | 1 | 972 | 1 |
| 18 | 7 | 34 | 1 | 58 | 1 | | |

Total of 6,885 fruits on 252 plants. Average, 27·3 fruits per plant.

15 per cent, whilst other germination tests have yielded up to 66 per cent. Even therefore if the average be near the latter figure the reproductive capacity of this species would appear to be less than 100 potential offspring per plant. The marked variations in the recorded germinations of the seeds of this species are perhaps connected with its mycorrhizal habit.

Wild Flax, *Linum alpinum* v. *anglicum* (*L. anglicum* Mill.; *L. perenne* auct.)

This, possibly endemic, Flax from East Anglia affords an interesting comparison with *L. catharticum*. The latter is a summer annual, whereas *L. alpinum v. anglicum* is a perennial, inhabiting similar semi-open communities of short turf on the chalk as its congener. But whereas *L. catharticum* is widespread on the chalk and occurs in other habitats, as, for instance, on calcareous dunes, the perennial species is extremely local.

The number of fruits was determined for forty specimens, as shown in Table LXXIV.

TABLE LXXIV. VARIATION IN NUMBER OF FRUITS PER PLANT OF *LINUM ALPINUM V. ANGLICUM*

| Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals |
|---|---|---|---|---|---|---|---|
| 3 | 2 | 13 | 3 | 24 | 4 | 40 | 1 |
| 4 | 1 | 14 | 1 | 25 | 1 | 42 | 1 |
| 5 | 1 | 15 | 2 | 27 | 1 | 64 | 1 |
| 8 | 2 | 17 | 1 | 31 | 1 | 68 | 1 |
| 10 | 1 | 18 | 2 | 32 | 1 | 75 | 1 |
| 11 | 1 | 20 | 1 | 36 | 1 | 88 | 1 |
| 12 | 4 | 22 | 1 | 39 | 1 | 105 | 1 |

Total of 1,046 fruits on 40 plants.

The average number of fruits was 26·1±2·45 ($\sigma$ 23·2; S.E.M. 3·68). The number of seeds was counted in twelve capsules selected at random, and ranged from six to ten (6 (2), 7 (0), 8 (5), 9 (3), 10 (2)). The average number of seeds was 8·25±0·25 ($\sigma$ 1·39; S.E.M. 0·4). The average seed output would therefore be 216±27 seeds per plant per annum, or between 189 and 243 seeds. Germination tests yielded very uniform results, and the average was 75 per cent, so that the average reproductive capacity would be about 162 potential offspring per plant per annum. It is thus apparent that the potential productivity of the perennial species is appreciably greater than that of the annual congener, despite the much higher frequency of the latter.

### Mouse-ear Chickweed, *Cerastium triviale* L.

This species offers a comparison with its congener, *C. glomeratum*, of open habitats. The capsule production was determined for twenty-six plants growing in short, semi-open herbage. The number of capsules ranged from 36 to 540, and totalled 4,372, an average of 168·1±16·5 capsules per plant per annum ($\sigma$ 123·8; S.E.M. 24·47).

The number of seeds per capsule was determined for twenty-five fruits, and ranged from 9 to sixty-two. The average was 38·3±2·25 seeds per capsule ($\sigma$ 16·7; S.E.M. 3·34).

These data indicate an average seed output of 6,463±1,009, equivalent to a seed weight of between 0·965 gm. and 1·32 gm. Here also, although the mortality risks of the perennial species might be expected to be less, the seed output per annum is higher than for the annual congener.

### *Moenchia erecta* Sm.

This is a species of very short, semi-open turf usually on gravelly or sandy soil, and the seedlings, which appear in the early autumn, only have to contend with a minimum of shading by surrounding vegetation. The average seed weight is 0·0009 gm.

The fruits produced by individual plants was determined for 217 specimens and ranged from one to twelve, as in Table LXXV.

TABLE LXXV. VARIATION OF FRUITS PER PLANT OF *MOENCHIA ERECTA*

| Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|
| 1 | 94 | 7 | 9 |
| 2 | 34 | 8 | 2 |
| 3 | 22 | 9 | 2 |
| 4 | 27 | 10 | 1 |
| 5 | 12 | 11 | 2 |
| 6 | 11 | 12 | 1 |

Total of 603 fruits on 217 plants.

The average number of capsules per plant was 2·8±0·1 ($\sigma$ 2·2; S.E.M. 0·16), but it will be noted that the modal number of capsules is one, the individuals with a single fruit representing over 43 per cent of the entire population. The variation curve is indeed very similar to that for *Silene conica*.

The number of seeds was counted in twenty capsules, and varied as follows: 31 (1), 33 (1), 34 (1), 36 (2), 37 (1), 40 (2), 42 (1), 45 (1), 46 (1), 51 (1), 52 (2), 55 (2), 56 (1), 57 (1), 59 (1), 60 (1). A total of 917 seeds, or an average of $45{\cdot}8 \pm 1{\cdot}4$ seeds per capsule ($\sigma$ 9·3; S.E.M. 2·1). Thus the average output of seeds per plant is $128 \pm 8$. The average weight of seed per plant is 0·1152 gm.

## Deptford Pink, *Dianthus Armeria* L.

This is a plant of dry banks and well-illuminated spots at the margins of scrub, and in coppiced woodlands on gravelly soil where the vegetation is sparse. The data in Table LXXVI respecting one hundred and thirty-one individuals shows that, as might be anticipated from the type of habitats frequented, there is a marked preponderance of small plants, the mode being individuals bearing six capsules, although the average number of fruits for the entire population is twenty-three ($22{\cdot}8 \pm 1{\cdot}52$; $\sigma$ 26·0; S.E.M. 2·28).

TABLE LXXVI. VARIATION IN NUMBER OF FRUITS PER PLANT OF *DIANTHUS ARMERIA* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 15 | 2 | 29 | 1 | 55 | 1 |
| 2 | 2 | 16 | 4 | 30 | 3 | 60 | 1 |
| 3 | 2 | 17 | 1 | 31 | 1 | 70 | 1 |
| 4 | 8 | 18 | 4 | 32 | 1 | 71 | 1 |
| 5 | 6 | 19 | 2 | 35 | 1 | 73 | 1 |
| 6 | 12 | 20 | 3 | 36 | 2 | 104 | 1 |
| 7 | 6 | 21 | 0 | 38 | 1 | 106 | 1 |
| 8 | 4 | 22 | 4 | 40 | 1 | 107 | 1 |
| 9 | 4 | 23 | 1 | 42 | 1 | 114 | 1 |
| 10 | 7 | 24 | 2 | 45 | 2 | 133 | 1 |
| 11 | 2 | 25 | 2 | 48 | 1 | 144 | 1 |
| 12 | 8 | 26 | 3 | 50 | 1 | | |
| 13 | 2 | 27 | 1 | 51 | 1 | | |
| 14 | 4 | 28 | 3 | 52 | 2 | | |

Total of 2,984 capsules on 131 plants. Average $22{\cdot}8 \pm 1{\cdot}52$.

The number of seeds was counted in twenty-five capsules, and ranged from 15 to 76 (15, 31, 36, 41, 47, 53 (2), 54, 55, 56, 57, 58 (2), 59, 60 (2), 61 (2), 62, 64, 65, 71, 73, 74, 76). The average number of seeds was $56 \pm 1{\cdot}8$ ($\sigma$ 13·5; S.E.M. 2·7). From these data the average seed output is therefore $1{,}279 \pm 126$ seeds per plant, or approximately between 1,150 and one thousand four hundred. Germination, according to Mitchell (1926, *Bot. Gaz.*) is from 8 to 31 per cent in the dark and from 79 to 88 per cent in the light. If we take the average germination to be about 84 per cent then the average reproductive capacity would be 1,074 potential offspring per plant.

## Clary, *Salvia verbenaca* L.

This species, like the preceding one, is associated with dry habitats, but particularly near the sea, and whereas *Dianthus Armeria* is biennial or annual

*Salvia verbenaca* is a perennial, which, from the size of the rootstock of plants on some dune systems, must attain a considerable age. Thirty-two plants of this species were examined for fruit production, and the number of schizachenes ranged from 168 to five thousand seven hundred and sixty. The average number per plant was $803 \pm 136$ ($\sigma$ 1,145; S.E.M. 204). The average germination is probably about 84 per cent, as tests yielded from 82 to 86·3 per cent; this would imply an average reproductive capacity of about 670 potential offspring per plant per annum.

Water Lobelia, *Lobelia Dortmanna* L.

This aquatic plant occurs in the semi-open community with *Littorella lacustris* in the early phases of succession on gravelly lake bottoms. The plants usually bear a single inflorescence, sometimes two. Examination of a number of fruiting specimens showed a range of from 1 to six capsules per plant, but the average number appeared to be two. The seeds were counted in eight capsules, and varied from 41 to 175 (41, 100, 101, 106, 108, 154, 161, 175). The average number of seeds per capsule was $118 \pm 9{\cdot}5$ ($\sigma$ 40·5; S.E.M. 14·3). It would then appear that each year a plant normally produces about 236 seeds and that the maximum output does not probably exceed 700 seeds.

It may be mentioned that the associate of *L. Dortmanna*, *Littorella lacustris*, also has a low seed output, but its vegetative mode of propagation ensures the rapid extension of the individuals arising from seed.

Rampion, *Phyteuma tenerum* Schulz. (*Phyteuma orbiculare* Auct. Angl.)

It appears probable that, although this species is found growing in close and not very short turf, it colonizes in the semi-open condition, but subsequently can persist in much taller and denser herbage by virtue of the considerable reserves present in the extensive and fleshy tap-root. The species has therefore been included here, although it is recognized that it might almost, but not perhaps with quite equal propriety, be placed with those of closed communities.

The number of seeds per capsule in twenty-one fruits ranged from 1 to 16, with an average of 8·2. The number of capsules per inflorescence in the specimens studied varied from 8 to 47, with a mean value of twenty-one. The number of inflorescence per plant was counted on fifty-six specimens growing in turf, and varied from 1 to 9 (1 (6), 2 (20), 3 (13), 4 (5), 6 (3), 7 (1), 8 (2), 9 (1)). It would appear, then, that the average output of seeds per plant is about five hundred and eighty. It should, however, be emphasized that in the absence of competition the number of seeds produced by a large plant may be nearly ten times the average output mentioned. The germination appears to be low, and perhaps not more than about 10 per cent, which would imply a reproductive capacity of about sixty. Possibly the correct conditions for germination were not realized, but Kinzel obtained only 8 per cent germination for the allied *Phyteuma orbiculare*, and low percentage germinations are not infrequent in Campanulaceae.

From the accompanying summary (Table LXXVII) it is evident that the seed output of species of semi-closed communities is not notably different from

TABLE LXXVII. SUMMARY OF SEED OUTPUTS OF SPECIES OF SEMI-OPEN UNSHADED HABITATS

| Species | Average seed output | Average reproductive capacity |
|---|---|---|
| Scilla autumnalis | 34·6±1·4 | 28·7 |
| Scilla verna | 54·6±1·27 | 51 |
| Moenchia erecta | 128±8 | |
| Linum catharticum | 136±13 | Under 100 |
| Linum alpinum v. anglicum | 216±27 | 162 |
| Lobelia Dortmanna | 236±19 | |
| Cicendia filiformis | 291±34 | |
| Gentiana lingulata v. praecox (G. anglica Pugsley) | 295±38 | |
| Gentiana baltica | 325±23 | |
| Phyteuma tenerum | *ca.* 580 | ? 60 |
| Gentiana germanica | 623±46 | |
| Carlina vulgaris | 679±71 | |
| Salvia verbenaca | 803±36 | *ca.* 670 |
| Gentiana axillaris | 862±48 | |
| Dianthus Armeria | 1,279±126 | 1,074 |
| Erigeron acre | 2,147±182 | |
| Silene otites | 2,186±299 | 1,420 |
| Linaria repens | 5,328±1,309 | |
| Linaria purpurea | *ca.* 6,000 | |
| Cerastium triviale | 6,463±1,009 | |
| Hypericum humifusum | 6,829±787 | 4,165 |
| Chlora perfoliata | 9,219±1,305 | |
| Erythraea umbellata | 10,840±1,214 | *ca.* 10,000 |

Mean output for 23 species 2,379 seeds per plant.

that of the species of permanently open habitats, although in view of the higher average of the latter, viz. 3,053 as compared with 2,379, and the higher outputs attained by individual species, the probability is that if there be a significant difference between the two categories it is the species of permanently open habitats that have the higher rate of potential reproduction. The mere fact of the association of species with semi-open rather than closed habitats suggests that the establishment of their seedlings may be restricted to the gaps in the plant covering, but it is clear that the risks of mortality are likely to be greater in a partially closed than in an open habitat; yet, as we have seen, there is no indication from the data given of a higher rate of reproduction—rather the reverse. This but adds to the evidence repeatedly furnished that shows the risks of mortality not to be the main factor governing potential reproduction of a species. On the other hand it is noteworthy that the chances of the seeds of a species of a permanently open habitat reaching a suitable locus for establishment is obviously far greater than for the seeds of species of partially open habitats. We would suggest that natural selection has tended to encourage a seed output *in excess* of that requisite to meet normal mortality risks, and that this excess will only have survival value so long as it bears an approximate relation to the average chances of establishment. The chances of establishment being necessarily greater for species of open habitats than for species of partially closed habitats it is in complete accord with the views just stated that the latter should possess a more restricted

output, in spite of the higher mortality risks. If this thesis be valid, we should expect that species of closed communities would have still lower reproduction rates.

## Species of Closed Communities

In the choice of species for study in closed communities the almost complete absence of any but perennial species renders comparison with the open and semi-open habitats somewhat difficult, in view of the preponderance of annual species in these latter. Further, the general absence of special means of vegetative multiplication in open habitat species, and their not infrequent presence in the perennial species of closed habitats, is a further complication that moreover may render difficult the demarcation of individual limits.

### Daisy, *Bellis perennis* L.

Although spreading vegetatively the rate of increase is insufficient to preclude *Bellis perennis* from consideration. The frequent appearance of this species in the continuous sward of lawns, etc., but its normal absence from true meadows indicates that whilst it is a colonizer of closed communities, and therefore the seedlings must have a considerable toleration of competition for nutrients and/or water, they are evidently intolerant of competition for light.

The number of achenes produced by the capitula of this species were counted in twenty-five fruiting heads, and ranged from 58 to 185 (58, 73, 83, 100, 101, 111 (2), 113, 118 (2), 119, 120, 124, 126 (2), 131, 134, 137, 143, 146, 153, 154, 159, 185, 187). The average was 125·2±4·0 ($\sigma$ 29·7; S.E.M. 5·94).

A total of 250 plants were examined for the production of fruiting capitula. The largest number of such found on any one plant was 32, but it is realized that since usually the largest specimens can only be identified as single individuals by digging them up some such may have been overlooked. Nevertheless the normal distribution of the data, as shown in Table LXXVIII, gives one confidence in the validity of the estimates based upon them.

TABLE LXXVIII. VARIATION IN NUMBER OF FRUITING CAPITULA PER PLANT OF *BELLIS PERENNIS* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 8 | 21 | 15 | 6 | 22 | 1 |
| 2 | 6 | 9 | 18 | 16 | 7 | 23 | 2 |
| 3 | 13 | 10 | 16 | 17 | 5 | 24 | 2 |
| 4 | 15 | 11 | 16 | 18 | 7 | 25 | 1 |
| 5 | 10 | 12 | 11 | 19 | 5 | 26 | 1 |
| 6 | 20 | 13 | 19 | 20 | 2 | 28 | 1 |
| 7 | 22 | 14 | 16 | 21 | 2 | 32 | 2 |

Total of 2,583 fruiting capitula on 250 plants.

The average number of fruit-heads per plant was thus 10·3±0·24 ($\sigma$ 5·65; S.E.M. 0·358).

The mean number of achenes per plant is therefore 1,288±71, the average weight of achenes per plant being between 0·197 gm. and 0·22 gm. Only one germination test was made, and this yielded 53 per cent. If representative, this would mean a reproductive capacity of about 680 per plant.

Dandelion, *Taraxacum officinale* L.

The specimens examined were all growing in meadowland in competition with grass. A total of 400 individuals were examined for fruiting capitula, the data for which are furnished in Table LXXIX.

TABLE LXXIX. VARIATION IN NUMBER OF FRUIT-HEADS PER PLANT OF *TARAXACUM OFFICINALE* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 2 | 13 | 23 | 25 | 3 | 37 | 2 |
| 2 | 6 | 14 | 16 | 26 | 4 | 38 | 4 |
| 3 | 14 | 15 | 11 | 27 | 5 | 42 | 1 |
| 4 | 23 | 16 | 9 | 28 | 5 | 43 | 1 |
| 5 | 15 | 17 | 5 | 29 | 4 | 46 | 1 |
| 6 | 31 | 18 | 14 | 30 | 2 | 48 | 1 |
| 7 | 27 | 19 | 10 | 31 | 1 | 55 | 1 |
| 8 | 30 | 20 | 8 | 32 | 1 | 56 | 1 |
| 9 | 24 | 21 | 9 | 33 | 2 | 59 | 1 |
| 10 | 22 | 22 | 6 | 34 | 1 | | |
| 11 | 22 | 23 | 5 | 35 | 2 | | |
| 12 | 19 | 24 | 3 | 36 | 3 | | |

Total of 5,317 fruiting heads on 400 plants.

The average number of fruiting heads per plant is thus 13·3±2·9 ($\sigma$ 9·36; S.E.M. 0·434). The number of fruits per capitulum was determined for thirty-six fruiting heads. The total for the thirty-six heads was 6,440 achenes, and the number per capitulum ranged from 63 to 401 (63, 82, 99, 114, 121 (2), 129, 143, 144, 149 (2), 153, 157, 159 (2), 167, 170, 171, 172 (2), 173, 177, 178, 179, 180, 186, 196 (2), 200, 202, 208, 209, 225, 352, 384, 401). The average is 180 (178·9±7·8; $\sigma$ 69·9; S.E.M. 11·6) fruits per capitulum. Thus the average output per plant is 2,381±157, or approximately between 2,200 and 2,500 achenes. It is of interest to note that this estimate is, as might be anticipated, lower than those quoted by H. C. Long, viz. 3,153 and five thousand four hundred. According to Kempski the germination of this species is 88 per cent, and Gill (1938) gives 91 per cent, so that the average reproductive capacity would be about 2,100 potential offspring per plant per annum.

Ox-eye Daisy, *Chrysanthemum leucanthemum* L.

The number of inflorescences per plant was determined for one hundred individuals growing in meadowland (Table LXXX).

The average number of fruiting heads was 14·1±0·83 ($\sigma$ 12·5; S.E.M. 1·25). The number of fruits formed per fruiting head is appreciably less than the number of florets. The latter may be as many as 553 on a capitulum, and

TABLE LXXX. VARIATION IN NUMBER OF FRUITING CAPITULA PER PLANT OF *CHRYSANTHEMUM LEUCANTHEMUM* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 2 | 4 | 10 | 4 | 19 | 1 | 33 | 1 |
| 3 | 5 | 11 | 5 | 20 | 2 | 35 | 1 |
| 4 | 6 | 12 | 5 | 21 | 2 | 36 | 2 |
| 5 | 8 | 13 | 5 | 23 | 2 | 38 | 1 |
| 6 | 5 | 15 | 7 | 24 | 1 | 44 | 1 |
| 7 | 5 | 16 | 2 | 25 | 1 | 57 | 1 |
| 8 | 0 | 17 | 5 | 29 | 2 | 90 | 1 |
| 9 | 10 | 18 | 4 | 31 | 1 | | |

Total of 1,410 fruiting heads on 100 plants.

most capitula bear over 200 florets, but the number of apparently fertile fruits, as judged by visual inspection, averaged only 192±19, and varied between 111 and two hundred and ninety. Thus, the number of achenes per plant would average 2,723±472. Actually an estimate by Maier-Bode of between 1,300 and 4,000 agrees fairly well with the average here arrived at. Germination averages about 94 per cent, so that the average reproductive capacity would be about 2,688 potential offspring per plant per annum.

Field Rush, *Luzula campestris* DC.

Forty-nine plants of this species were examined for fruit production, and yielded a total of 7,779 capsules, almost all of which contained three seeds. The range was from 23 capsules to 853 on the individual plants, and the average number of seeds per plant 476±45($\sigma$ 516; S.E.M. 73·7), that is, between 471 and 561 seeds per plant per annum. The average weight of a seed is 0·00066 gm., so that the average weight of seed per plant is between 0·31 gm. and 0·37 gm.

Self-heal, *Prunella vulgaris* L.

Although only a few specimens of this species have been examined, the average they yield of 854 schizachenes per plant is so close to the mean of the small and large plants examined by Eklund (600–1,000) that it is probably of value as a rough approximation. The average germination appears to be about 70 per cent, so that the average reproductive capacity would be about 600 potential offspring per plant per annum.

Meadow-sage, *Salvia pratensis* L.

Only nine plants of this rare British species were available for study. The number of schizachenes on these plants was as follows: 276, 2,304, 2,956, 3,333, 4,348, 5,220, 5,760, 6,744, 10,509; a total of 41,450, or an average of 4,605 achenes per plant per annum.

The average germination is about 61 per cent, so that the average reproductive capacity would be about 2,800 potential offspring per plant per annum.

*Senecio campestris* DC.

A total of forty-nine plants were examined for the number of fruiting capitula produced, which varied from one to seven (1 (3), 2 (10), 3 (13), 4 (11), 5 (6), 6 (5), 7 (1)). The average is 3·53±0·13. The fruits were counted on ten fruiting heads and varied as follows: 56, 57, 66, 70, 74 (2), 76 (2), 85, 87. The average number of fruits per capitulum was thus 72·1±1·9 ($\sigma$ 9·7; S.E.M. 2·9). Hence the mean seed output is 255±15 per plant.

Germination tests indicate an average of between 70 and 80 per cent, so that the reproductive capacity probably averages 191±10 potential offspring per plant.

There are grounds for believing that *S. campestris* may often be monocarpic, since most plants in the writer's own garden died after flowering, and the very marked fluctuations in population of this species in successive years in the natural habitats also point to the same feature. It is at most a short-lived perennial.

Clustered Bell-flower, *Campanula glomerata* L.

The number of capsules developed upon individual plants was determined for forty individuals, and varied as shown in Table LXXXI. The range is seen to be wide, namely from 3 to 264, the average being 30±4·8 ($\sigma$ 46·3; S.E.M. 7·3).

TABLE LXXXI. VARIATION IN NUMBER OF CAPSULES PER PLANT OF *CAMPANULA GLOMERATA*

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 3 | 1 | 11 | 1 | 22 | 1 | 37 | 1 |
| 4 | 2 | 13 | 1 | 23 | 3 | 40 | 1 |
| 5 | 5 | 14 | 4 | 24 | 3 | 74 | 1 |
| 6 | 1 | 16 | 2 | 25 | 1 | 102 | 1 |
| 8 | 2 | 18 | 1 | 30 | 1 | 150 | 1 |
| 9 | 1 | 20 | 1 | 34 | 1 | 264 | 1 |
| 10 | 2 | 21 | 1 | 35 | 1 | | |

Total of 1,202 capsules on 40 plants. Average 30·05.

The seeds were counted in sixteen capsules (11, 61, 62, 65, 68, 70, 71, 72, 76, 78, 88, 91, 94, 98, 102, 106); these gave an average of 76±3·6 seeds per capsule ($\sigma$ 21·7; S.E.M. 5·4). Eklund gives the number of seeds in a single capsule only, but this was much higher, namely two hundred and fifty. This figure of Eklund's is far outside the range of our own observations.

On the data given here the average seed output would be 2,297±473 seeds per plant per annum. If we accept Kinzel's figure of 10 per cent germination for this species, the average reproductive capacity is 230 potential offspring per plant each year.

Cat's-ear, *Hypochoeris radicata* L.

The number of capitula on meadow plants of this species ranged from 3 to 56, with an average of 22±4·3. The average number of achenes per capitulum was 44, so that the average number of achenes per plant is about nine hundred and seventy. The percentage germination is somewhat variable.

It may be as low as 33 per cent or over 90 per cent, and the mean reproductive capacity is probably of the order of 600 potential offspring per plant per annum.

Nodding Thistle, *Carduus nutans* L.

This thistle normally occurs in relatively open habitats but can also colonize short grass. The fruiting capitula on forty-three plants were as follows: 5 capitula (1), 6 (1), 7 (1), 10 (1), 11 (3), 12 (1), 13 (5), 14 (2), 15 (1), 16 (4), 18 (3), 19 (1), 20 (1), 21 (1), 22 (4), 23 (2), 25 (1), 26 (1), 28 (1), 29 (1), 30 (2), 34 (2), 35 (2), 36 (1). A total of 841 fruit-heads, or an average of $19{\cdot}5 \pm 0{\cdot}85$ ($\sigma$ 8·3; S.E.M. 1·27).

The achenes per capitulum were counted in twelve examples selected at random, and numbered 151, 155, 188, 190, 194, 204, 207, 211, 220, 242, 246, 299; a total of 2,507 achenes, or an average of $209 \pm 7{\cdot}6$ ($\sigma$ 38·7; S.E.M. 11·38). The output of fruits per plant was therefore $4{,}082 \pm 326$.

The average weight of an achene is 0·00223 gm., which implies an average output per plant of 9·1 gm.

Greater Knapweed, *Centaurea scabiosa* L.

There are two varieties of this species: the one, which is the commoner, with urceolate receptacles and inner phyllaries with more rounded laminae and more divergent appendages (Fig. 26); the other, with smaller heads, narrower and more elongated in form, and with inner phyllaries that have more elliptical laminae (Fig. 26) is apparently rare.

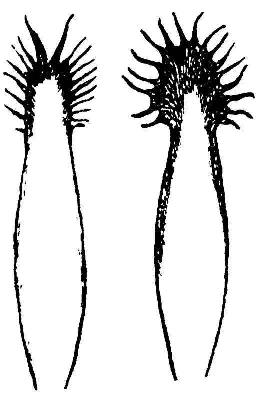


FIG. 26. Inner Phyllaries of the Greater Knapweed (*Centaurea scabiosa*). On the right that of the common variety, on the left that of the uncommon narrow-headed variety.

An insufficient number of specimens of the second variety were available for examination, but the average number of capitula were appreciably fewer than in the common variety, whilst the number of achenes per capitulum are much fewer, and in the specimens examined varied from 20 to 38, with an average of about thirty.

The common variety has an average of about 65 achenes per capitulum, and the number in the specimens examined ranged from 37 to eighty-seven.

Fifty-seven plants of the common variety were examined for the number of fruiting capitula, which varied as follows: 3 capitula (1), 4 (1), 5 (1), 6 (1), 8 (1), 9 (4), 10 (2), 11 (2), 12 (4), 13 (1), 14 (1), 16 (1), 17 (2), 18 (2), 19 (1), 20 (1), 21 (1), 22 (3), 23 (1), 28 (1), 30 (2), 33 (1), 34 (1), 35 (2), 36 (2), 39 (1), 44 (1), 46 (1), 47 (1), 51 (1), 52 (2), 55 (1), 56 (1), 57 (1), 64 (2), 65 (1), 66 (2), 92 (1), 118 (1). Thus, a total of 1,744 capitula, or an average of $30{\cdot}6 \pm 0{\cdot}65$ fruiting heads per plant ($\sigma$ 7·4; S.E.M. 0·98).

The total output of achenes per plant is therefore about 2,000 per annum. It must, however, be emphasized that the capitula are not infrequently galled by *Urophora solstitialis*, and examination of the fruits often reveal that the contents have been eaten. This applies equally to both varieties.

Although, as mentioned above, the output of the uncommon variety has not been accurately determined, it seems probable that it is not more than about one-quarter of the common type, so that here too we have a parallelism between output and frequency.

Chalk Scabious, *Scabiosa columbaria L.*

This characteristic chalk down rosette plant is a colonizer of short turf, though it can persist for some time after grazing ceases. Eighty-nine plants were examined for fruiting capitula, as shown in Table LXXXII.

TABLE LXXXII. VARIATION IN NUMBER OF FRUITING CAPITULA OF *SCABIOSA COLUMBARIA*

| Number of heads | Number of plants | Number of heads | Number of plants |
|---|---|---|---|
| 1 | 5 | 12 | 3 |
| 2 | 11 | 15 | 2 |
| 3 | 11 | 16 | 1 |
| 4 | 11 | 18 | 1 |
| 5 | 9 | 20 | 1 |
| 6 | 10 | 21 | 3 |
| 7 | 5 | 26 | 1 |
| 8 | 5 | 27 | 1 |
| 9 | 3 | 29 | 1 |
| 11 | 4 | 31 | 1 |

A total of 651 fruiting heads, or an average of $7{\cdot}31 \pm 0{\cdot}46$ ($\sigma$ 6·5; S.E.M. 0·69). The number of fruits per head ranged from 23 to 59, with an average of $42{\cdot}4 \pm 2{\cdot}38$. Thus, the output of the single-seeded fruits is $311 \pm 47$.

Hoary Plantain, *Plantago media* L.

This species, although colonizing closed communities of short turf, probably does so only in the more open parts, and it is possible that it should be placed amongst those of semi-open rather than closed communities as regards its capacity for invasion. This is the more likely in view of the small size of the seeds. It is probable, however, that it can colonize a closed habitat, provided the herbage be short, so that the shading is negligible.

A total of 106 plants growing in chalk pasture showed a range in the number of fruiting spikes of from 1 to 31, with an average of $4 \pm 0{\cdot}27$ ($\sigma$ 4·1; S.E.M. 0·405). The number of fruits on a spike ranged from 52 to 130, with an average of $79{\cdot}7 \pm 5{\cdot}7$. Each capsular fruit contained from two to four seeds, but by far the greater number contained three. Thus, the average number of seeds per plant was $960 \pm 132$, with a maximum estimated output of seven thousand four hundred and forty.

## Damp Habitat Species

Marsh Marigold, *Caltha palustris* L.

A comparatively small number of plants of this meadow species were examined for fruit production, the number of fruiting heads ranging from 11 to 53 per plant with an average of $28 \pm 1{\cdot}8$ fruit-heads per plant.

Examination of a large number of immature and mature follicles showed that a considerable proportion of the ovules normally abort. The number of ovules appears to be usually about 17 or 18 but, as the following data show, the number of seeds is usually much fewer.

TABLE LXXXIII. VARIATION IN NUMBER OF SEEDS PER FOLLICLE OF *CALTHA PALUSTRIS* L.

| Number of ripe seeds | Number of follicles | Number of ripe seeds | Number of follicles |
|---|---|---|---|
| 1 | 4 | 11 | 18 |
| 2 | 7 | 12 | 14 |
| 3 | 3 | 13 | 8 |
| 4 | 12 | 14 | 6 |
| 5 | 4 | 15 | 7 |
| 6 | 7 | 16 | 2 |
| 7 | 8 | 17 | - |
| 8 | 9 | 18 | 1 |
| 9 | 21 | 19 | 1 |
| 10 | 17 | | |

Total of 1,352 seeds in 149 follicles. Average $9{\cdot}07 \pm 0{\cdot}25$.

TABLE LXXXIV. VARIATION IN NUMBER OF FOLLICLES PER FRUIT OF *CALTHA PALUSTRIS* L.

| Number of follicles | Number of fruits | Number of follicles | Number of fruits |
|---|---|---|---|
| 3 | 1 | 8 | 23 |
| 4 | 5 | 9 | 13 |
| 5 | 18 | 10 | 10 |
| 6 | 26 | 11 | 6 |
| 7 | 20 | 14 | 1 |

Total of 890 follicles in 123 fruits. Average $7{\cdot}23 \pm 0{\cdot}12$.

The data furnished show that the number of seeds per follicle has a mean value of $9{\cdot}07 \pm 0{\cdot}25$ ($\sigma$ 3·83; S.E.M. 0·38), whilst the number of follicles per fruit has a mean value of $7{\cdot}23 \pm 0{\cdot}12$ ($\sigma$ 1·95; S.E.M. 0·177). Thus each fruit-head normally produces between 62 and 68 seeds. From these data the average seed output would be $1{,}832 \pm 209$ seeds per plant per annum.

Seeds sown as soon as they were shed yielded an average of 40 per cent germination, but as all the seeds tested were obtained from the same locality this figure may not be representative. If it is, the average reproductive capacity would be 764 potential offspring. In these tests all the seeds which germinated did so within 27 days, but Mr. Dymes informs me that he has obtained germination both in the autumn and the following spring. The average seed weight is 0·0011 gm. The average output weight would therefore be about 2·1 gm.

## Ragged Robin, *Lychnis flos-cuculi* L.

This is another damp meadow species of which only a small number of individuals were examined for fruit production. The number of capsules ranged from 23 to 324 with an average of $57 \pm 20$, but, owing to the exceptionally large plant, this figure is unduly high, and it is probable that the average for a much larger population would be nearer forty fruits per plant. The seeds

were counted in sixteen capsules and yielded: 65, 85, 95, 101, 104, 108, 109, 115, 117, 121 (2), 123, 129, 131, 133, 151, or a total of 1,808 seeds and an average of $113 \pm 3{\cdot}3$ ($\sigma$ 19·6; S.E.M. 4·9). If we accept forty as a rough approximation of the number of fruits, the average seed output would be about 4,500 seeds, a fairly high figure, and it is therefore of interest to note that *L. flos-cuculi* is a rather short-lived perennial and tends to colonize where competition for light is temporarily diminished. It is in fact an opportunist species and should perhaps more properly be placed in the category of species of intermittently available habitats. Vegetative propagation by means of offsets also occurs.

Marsh Sow Thistle, *Sonchus palustris* L.

Of this rare fen species eleven fruiting plants were examined, and the number of fruiting heads ranged from fifteen to one hundred and sixty-three; the average was $64 \pm 9{\cdot}6$ fruiting capitula per plant. The achenes were counted on nine capitula selected at random from two plants; these numbers were: 46, 75, 79, 80, 94, 95, 107, 108, 122. The average was thus $90 \pm 5{\cdot}2$ fruits per capitulum. The average number of fruits per plant was thus $5{,}810 \pm 1{,}197$. Only one batch of seeds was tested for germination and yielded an average of 73 per cent which, if representative, would imply a reproductive capacity of approximately 4,200. The fruits weigh 0·000943 gm., so that the average output weight would be about 5·5 gm.

Bird's-eye Primrose, *Primula farinosa* L.

This northern species of damp pastures, especially those of a basic character, is locally abundant. One hundred and twenty-seven plants were examined for capsule production, in the Craven district of Yorkshire and in Teesdale, which yielded a total of 468 capsules as follows:

| Capsules per plant | Number of plants | Capsules per plant | Number of plants |
|---|---|---|---|
| 1 | 8 | 6 | 4 |
| 2 | 24 | 7 | 7 |
| 3 | 36 | 8 | 4 |
| 4 | 25 | 9 | 1 |
| 5 | 18 | | |

Average $3{\cdot}68 \pm 0{\cdot}1$.

The average number of capsules per plant was thus $3{\cdot}68 \pm 0{\cdot}1$ ($\sigma$ 1·7; S.E.M. 0·15).

The average number of seeds per capsule was determined by J. Scott (1880, p. 117) as fifty-four, so that the average seed output would be $199 \pm 5$ seeds per plant. The average output weight would be about 0·018 gm.

Heath Lobelia, *Lobelia urens* L.

This rare oceanic species of damp heaths is essentially a colonizer of well-illuminated places, and the rosette habit and its minute seeds are in conformity with this feature. Miss Joan Ivimy and Mrs. Steen have carried out experiments which show that germination in darkness is low, varying from

0 to 32 per cent with an average of 14 per cent, whereas the average in light was 62 per cent and may be as high as 96 per cent.

The capsules were counted on twenty-three plants and ranged from 20 to 162 (20, 25, 26, 29, 37, 38, 40, 41, 43, 48, 48, 49, 54, 57, 60, 63, 77, 83, 107, 116, 124, 152, 162). The average number of capsules was thus 65±5·5 ($\sigma$ 39·5; S.E.M. 8·2). The numbers of seeds in ten capsules were 65, 125, 129, 131, 142, 146, 168, 174, 176, 192. Average 144·8±7·3 ($\sigma$ 34·3; S.E.M. 11·0). The average seed output is thus 9,452±1,271, and the average reproductive capacity about 5,860 potential offspring per annum. As the seeds weigh 0·000013 gm., the average output weight is 0·1229 gm.

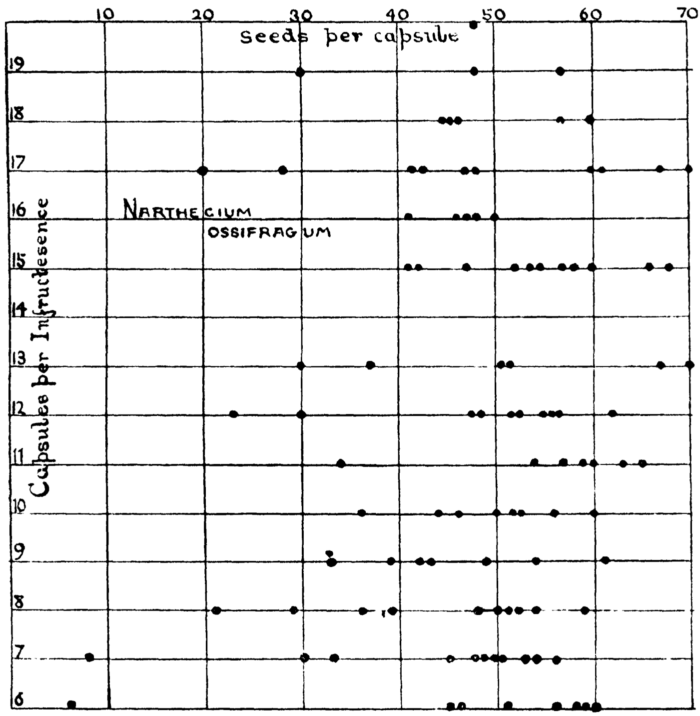



FIG. 27. Graph showing relation between the number of seeds per capsule in 103 capsules and the number of capsules comprising the infructescence of the Bog Asphodel (*Narthecium ossifragum*)

*Saxifraga stellaris* L.

This Saxifrage, which is a species of well-illuminated situations, especially at the margins of upland rills, is a rosette plant. The number of capsules produced on an inflorescence ranged from two to seven, with an average of 4±0·55. The seeds in the capsules examined ranged from twenty-nine to one hundred and sixty, with an average of 97±10·7 seeds per capsule. Thus the number of seeds per infructescence had a mean value of 394±96.

Bog Asphodel, *Narthecium ossifragum* Huds.

Owing to the vegetative spread of this species the limits of individuals are not usually determinable. It would appear to be a colonizer of open situations

on damp peaty soil, and although, once established, capable of extending in comparatively dense vegetation, is perhaps a colonizer of intermittently available habitats.

The number of capsules was determined for one hundred infructescences as follows:

TABLE LXXXV. VARIATION IN NUMBER OF CAPSULES PER INFRUCTESCENCE OF *NARTHECIUM OSSIFRAGUM* Huds.

| Number of capsules | Number of infructescences | Number of capsules | Number of infructescences | Number of capsules | Number of infructesences |
|---|---|---|---|---|---|
| 6 | 1 | 11 | 19 | 16 | 6 |
| 7 | 3 | 12 | 14 | 17 | 8 |
| 8 | 4 | 13 | 9 | 18 | 2 |
| 9 | 8 | 14 | 5 | 19 | 1 |
| 10 | 12 | 15 | 7 | 20 | 1 |

Total of 1,237 capsules. Average 12·37±0·2.

Taking the mean number of capsules per infructescence as 12·4, the standard deviation is 2·96 and the standard error of the mean 0·296.

The seeds are long (*ca.* 8 mm.) and narrow with a small body and an extended testa which renders the seed readily carried by air currents (*cf.* Fig. 1). The average weight of the seeds is 0·0001005 gm.

The seeds were counted in one hundred capsules and totalled 4,871, or an average of approximately 49±0·8 seeds per capsule ($\sigma$ 12·1; S.E.M. 1·21).

TABLE LXXXVI. VARIATION IN NUMBER OF SEEDS PER CAPSULE OF *NARTHECIUM OSSIFRAGUM*

| Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules | Number of seeds | Number of capsules |
|---|---|---|---|---|---|---|---|
| 6 | 1 | 37 | 1 | 50 | 5 | 61 | 2 |
| 8 | 1 | 39 | 2 | 51 | 4 | 62 | 1 |
| 20 | 1 | 41 | 2 | 52 | 6 | 63 | 1 |
| 21 | 1 | 42 | 3 | 53 | 1 | 65 | 1 |
| 22 | 1 | 43 | 1 | 54 | 6 | 66 | 1 |
| 28 | 1 | 44 | 1 | 55 | 1 | 67 | 2 |
| 29 | 1 | 45 | 4 | 56 | 5 | 68 | 1 |
| 30 | 3 | 46 | 4 | 57 | 3 | 70 | 2 |
| 33 | 2 | 47 | 4 | 58 | 3 | | |
| 34 | 1 | 48 | 8 | 59 | 3 | | |
| 36 | 2 | 49 | 1 | 60 | 6 | | |

Total of 4,871 seeds in 100 capsules.

Thus the average number of seeds produced per infructescence would be 607±19. The large patches formed by plants of this species are quite often relatively barren, so that the number of fruiting stems may be no greater than for much smaller plants. Six infructescences is probably about the average number per plant, and this would imply about 3,600 seeds. The correlation between seed number and capsule number is shown in Fig. 27, from which it is seen that such only obtains for the very depauperate specimens.

Yellow Iris, *Iris Pseudacorus* L.

The number of seeds is forty-five capsules of this species varied as follows: 13 (3), 18 (1), 20 (1), 21 (2), 22 (1), 23 (3), 25 (2), 27 (1), 28 (4), 29 (5), 31 (1), 32 (1), 33 (1), 34 (2), 36 (3), 37 (2), 38 (1), 40 (2), 41 (1), 42 (1), 43 (1), 44 (1), 45 (1), 48 (1), 49 (1), 53 (1), 60 (1), or a total of 1,433 seeds. The mean number was thus $32 \pm 1$ ($\sigma$ 10·4; S.E.M. 1·55).

A noteworthy feature of this species is that, whilst the majority of the seeds are closely packed and disk-like in form, the terminal seeds in each loculus are more or less plano-convex and often larger, and this is to some extent true also of those seeds which, though not terminal, are adjacent to ovules that have failed to develop.

In view of the advantages that have been shown to accrue to heavier seeds, we see here an indication that a high proportion of fertilized ovules may not necessarily be an unmitigated advantage, and indeed it would appear not improbable that a partial seed output, when accompanied by such increase in the weight of individual seeds, may not, in fact, be detrimental but promote establishment in less favourable situations where the food reserve in the smaller seeds would be inadequate to bring about effective colonization.

The average weight of over one hundred terminal seeds was 0·0634 gm., whilst the average weight of the non-terminal seeds from the same capsules was 0·0551 gm. Thus the terminal seeds showed an average weight of just over 15 per cent in excess of the intermediate seeds. According to Mr. T. A. Dymes (1920) about 20 per cent of the seeds shed in October germinate in the period from February to June of the next year, whilst 20 per cent more germinate in the following spring. Some of the seeds float readily, as they are light in weight owing to the replacement of some of the contained water by air, and of these the flattened seeds germinate rather more rapidly and better than the rounded seeds. But Dymes found no difference in the germination of the heavier seeds, whether flattened or rounded, both of which yield a higher germination than either type of light-weight seed. In unfavourable conditions one would expect the heavy rounded seeds to have the advantage, but in any circumstances the difference in weight, size, and shape would tend to bring about a differential dispersal.

Marsh Stitchwort, *Stellaria palustris* Retz. (*S. glauca* With.)

Twenty-six capsules of this species were examined and contained the following numbers of seeds: 7 (1), 9 (5), 10 (4), 11 (4), 12 (2), 13 (3), 14 (1), 15 (1), 18 (1), 22 (2), 23 (1), 27 (1). The average was $13{\cdot}07 \pm 0{\cdot}6$ ($\sigma$ 5·0; S.E.M. 0·9). As the plant does not usually bear many fruits the average seed output is probably small.

Bog Bean, *Menyanthes trifoliata* L.

This plant spreads mainly by means of the rhizomes which root freely at the nodes and may extend several yards in a single season. The number of capsules formed on an inflorescence may be as many as 25, but the everage number appears to be seventeen ($17 \pm 0{\cdot}35$). The number of seeds in the capsules examined ranged from four to thirty-one, with an average of $12{\cdot}7 \pm 0{\cdot}7$

($\sigma$ 7·2; S.E.M. 1·04). The average seed output per inflorescence would therefore appear to be 210±10.

Water Hemlock, *Cicuta virosa* L.

Only two specimens were examined, one of which appeared to be of average size and the second a large plant. The former yielded 12,720 mericarps and the second nearly 27,000 mericarps. Eklund gives the output, for a single specimen only, of this species as 20,700, so it would appear that the average might well be between fifteen and twenty thousand. Mr. B. T. Lowne informs me that he has obtained 55 per cent germination of the seeds of *Cicuta virosa*. It is evident then that the reproductive capacity is high, probably exceeding 8,000 and perhaps about 11,000. We would appear then to have here an example of a species which is decidedly rare in most parts of the country, although possessing a high reproductive capacity. It should, however, be emphasized that the Water Hemlock is one of the many aquatic and marsh species in the British flora which are far less common to-day than formerly (Salisbury, 1927). *Cicuta virosa* has, in fact, probably become extinct in five counties where it once grew, and has diminished in others. Hill, in his " British Herbal " of 1756, describes this plant as " common about our fen ditches and in watery places," under the name of Long-leaved Water Parsnip, and, despite the poverty of the illustrations of this work, the identity is unmistakable. About a century later Baxter (1840) refers to *Cicuta virosa* as being " not common." In the first edition of Hooker's " Students' Flora " it is described as local (Hooker, 1870), and even to-day, though generally rare or even very rare, it was within recent years still locally common in the fens of Norfolk (Nicholson, 1913). Its diminution is due to reduction of suitable habitats through drainage and deliberate destruction because of its extremely poisonous character.

Of the above damp habitat species all are encountered as adult plants in more or less closed communities. *Primula farinosa* is associated with well-illuminated habitats and possibly requires partially open conditions for colonization, but has been included in the following summary. *Lobelia urens* and *Narthecium ossifragum* certainly demand more or less open or unshaded conditions for primary establishment, and have been omitted. They might perhaps appropriately be regarded as species colonizing intermittently available habitats.

*Tofieldia palustris* Huds.

Fifty-six plants of this species were examined, and yielded a total of 487 capsules, as shown in table at top of following page.

The average number of capsules per plant was 8·7±0·2 ($\sigma$ 2·3; S.E.M. 0·3). The seeds in 48 capsules totalled 1,128, or an average of 23·4 seeds per capsule (23·4±0·6; $\sigma$ 6·3; S.E.M. 0·9). The average seed output is therefore 203±10 seeds per plant per annum. Only one germination test was carried out, and this gave an average of 13 per cent. If this is representative then the reproductive capacity would be about 26 potential offspring per plant per annum.

| Capsules | Plants |
|---|---|
| 4 | 2 |
| 5 | 2 |
| 6 | 6 |
| 7 | 7 |
| 8 | 8 |
| 9 | 14 |
| 10 | 6 |
| 11 | 4 |
| 12 | 2 |
| 13 | 4 |
| 14 | 1 |

| Seeds per capsule | Number of capsules | Seeds per capsule | Number of capsules |
|---|---|---|---|
| 11 | 1 | 25 | 5 |
| 15 | 2 | 26 | 1 |
| 16 | 3 | 27 | 1 |
| 19 | 3 | 28 | 1 |
| 20 | 1 | 29 | 1 |
| 21 | 1 | 30 | 1 |
| 22 | 3 | 33 | 1 |
| 24 | 8 | | |

Total of 743 seeds in 33 capsules.
An additional 15 capsules contained 385 seeds.

*Carum verticillatum* (L.) Koch.

Specimens of this species growing in the closed wet meadow community in West Scotland were examined, and yielded from 300 to 1,200 schizachenes per plant, with an average of seven hundred and sixteen.

Grass-of-Parnassus, *Parnassia palustris* L.

This species grows in two types of habitat, namely in wet meadow flushes, where the vegetation is more or less closed, and also in dune slacks, as on the Lancashire coast, where the community is an open one and competition much less marked. In the latter habitat the flowers are much larger and the number of flowers per plant more numerous. Culture of the two types side by side under identical conditions, however, gives no grounds for believing that *condensata* is hereditarily different, but is to be regarded as a habitat form induced by the conditions of nutrition and relative freedom from competition. The data here furnished do not include *forma condensata* (*var. condensata* Travis & Wheldon).

One hundred plants furnished the following numbers of fruits:

| Capsules | Individuals | Capsules | Individuals |
|---|---|---|---|
| 1 | 34 | 6 | 1 |
| 2 | 27 | 7 | 1 |
| 3 | 24 | 8 | 1 |
| 4 | 6 | 9 | 1 |
| 5 | 5 | | |

The average number of capsules was therefore $2{\cdot}39 \pm 0{\cdot}1$ capsules per plant ($\sigma$ 1·53; S.E.M. 0·153).

The seeds were counted from thirteen capsules, under a dissecting microscope, and the numbers, exclusive of seeds which from visual examination were obviously infertile, were as follows: 317, 388, 490, 558, 588, 717, 723, 775, 780, 820, 1,064, 1,168, and 1,338. A total of 9,726 seeds, or an average of $748 \pm 54$ ($\sigma$ 291; S.E.M. 80·8). The average seed output was therefore $1{,}792 \pm 203$, or approximately between 1,600 and 1,900 per plant per annum.

Kinzel gives the germination of this species as 76 per cent, which would imply a reproductive capacity of about 1,360 potential offspring per plant per annum. The seeds are minute and only weigh 0·000024 gm., so that the reproductive weight would be about 0·03 gm.

TABLE LXXXVII. SUMMARY OF DATA FOR SPECIES OF CLOSED COMMUNITIES

| | Average seed output | Average reproductive capacity |
|---|---|---|
| Ranunculus bulbosus | 69±3·3 | |
| Primula farinosa | 199±5 | |
| Tofieldia palustris | 203±10 | ? 26 |
| Senecio campestris | 255±15 | 191 |
| Scabiosa columbaria | 311±47 | |
| Luzula campestris | 476±45 | |
| Carum verticillatum | ? 716 | |
| Prunella vulgaris | 854 | 600 |
| Plantago media | 960±132 | |
| Hypochoeris radicata | 970 | 600 |
| Bellis perennis | 1,288±71 | 680 |
| Parnassia palustris | 1,792±203 | 1,360 |
| Caltha palustris | 1,832±209 | ? 764 |
| Centaurea Scabiosa | *ca.* 2,000 | |
| Campanula glomerata | 2,297±473 | ? 225 |
| Taraxacum officinale | 2,381±157 | 2,100 |
| Chrysanthemum leucanthemum | 2,723±472 | 2,688 |
| Carduus nutans | 4,082±326 | |
| Hypericum pulchrum | 4,449±518 | 3,692 |
| Salvia pratensis | 4,605 | 2,800 |
| Lychnis flos-cuculi | ? 4,500 | |
| Sonchus palustris | 5,810±1,197 | 4,200 |

Arithmetic mean of averages for 22 species 1,944 (seed output)
" " " 13 " 1,532 (reproductive capacity).

Whilst it is obvious that, having regard to the small number of species for which data have been obtained, the average may be misleading, it is nevertheless of interest, and perhaps significant, that just as the species of semi-closed habitats presented a lower average output of seeds than those of open habitats, so too those of closed communities present a lower average output than the species of semi-closed communities. So too we find a corresponding gradation with respect to the highest average seed outputs in these three categories; such consistency is remarkable if it be entirely fortuitous. These data for species of closed communities tend then to confirm the suggestion that the magnitude of the output of seed, in excess of that necessary for survival, is proportional to the opportunities which the natural habitat affords for establishment. It has, however, been already pointed out that competition itself reduces very markedly the seed output. In the instance of *Ranunculus bulbosus* the output from plants completely free from competition was almost ten times that of meadow specimens, whilst a plant of the *forma condensata* of *Parnassia palustris* growing more or less isolated was estimated to produce some 20,000 seeds, or over ten times the average number for that species. But this is true also of the species of open habitats, which are by no means free from competition both amongst themselves and from other individuals of the same species, and we have already cited the example of *Saxifraga tridactylites*, which, in the absence of competition, produced more than six times the seed output of the largest specimen from the normal environment. It is improbable, therefore, that competition alone accounts for the differences

observed, and even in its absence it appears likely that the seed production of the species characteristic of closed communities would be found to be less than that of species of open habitats grown under like conditions.

But it must be borne in mind that the species of the closed community are almost all perennial whereas those of the open habitats are mostly annual, hence, so far as persistence of the species is concerned, the perennials are clearly much better equipped than the annuals except in so far as the seed phase evades catastrophies in the habitat, whether natural or artificial. With increase in the output of seed the efficiency of the dispersal mechanism must increase also if the law of diminishing returns is not to operate to such an extent as to render such increase of little, if any, survival value. Hence it follows that the seed production of a species over and above that required to meet mortality risks will be more effective in a relatively stable environment if distributed over a period of years, and this is the more so the greater the density of the community and the larger the seed balance concerned. A very large output of seeds is usually associated with lightness of weight, in consequence of which the radius of dispersal is increased and the augmented output rendered effective, since, with the increase of numbers, there is also the increased area in which the seeds may find a suitable niche for their establishment. We have seen that with added density and height of the vegetation with which a species is usually associated the weight of the seed tends to be greater, so that dispersal of the unspecialized seeds or fruits tends to diminish, and thus a large output becomes less effective. It is, no doubt, related to this feature that the more specialized types of fruit and seed dispersal are particularly associated with the heavier types of propagules.

To cite but two examples from the Rubiaceae, the large fruits of the Woodruff (*Asperula odorata*) and the Goosegrass (*Galium aparine*) are beset with hooked bristles and efficiently dispersed by animals, whereas the small schizachenes of *Asperula cynanchica* and *Galium anglicum*, species of open habitats have no specialized mechanism for dispersal (*cf.* Fig. 3). *Galium aparine* is a species of the woodland marginal flora and of the scrub community, though secondarily it has become a cornfield weed. *Galium tricorne*, which has fruits that are only slightly smaller than those of *G. aparine* and are almost smooth, is primarily a plant of open habitats on basic soils, and is not only relatively uncommon, or even rare, but decidedly local also, being often absent from quite suitable areas, which attests to the inefficiency of its fruit dispersal.

The conception then of seed production which we have arrived at from an objective study of a number of species is that of an amount which transcends the needs of mere replacement, and has, by the processes of natural selection acting on survival value, become more or less adjusted as between the additional chances of colonization which an increased output might yield and the accompanying augmentation of the intensity of competition. Any increase in the efficiency of seed or fruit dispersal will enable a larger output to have survival value, whilst increase in weight of the individual propagules, though enabling a species to colonize more advanced communities, would normally imply the survival value of a smaller output, since the diminution

in effective dispersal would automatically involve an increased wastage, so that a much smaller seed production might have equal value to the species.

### Species of more or less Shady Habitats

The species which it is proposed to treat of in this category are those which are characteristic of woodlands but exclusive of those which, though associated with the woodland community, are essentially colonizers of the temporarily open habitats provided by coppiced areas, etc., and thus are more properly considered in the category of species of intermittently open habitats.

Dog's Mercury, *Mercurialis perennis* L.

Mukerji's study of this species (1930) showed that a single plant might produce an average of 300 seeds, but that of these the average germination was only 5 per cent. Hence the reproductive capacity by means of seeds would be some 15 potential offspring per plant per annum. The vegetative propagation of *Mercurialis* is, however, efficient and rapid.

Town-Hall Clock, *Adoxa moschatellina* L.

Here, too, vegetative propagation is rapid, but the production of seeds by the separated units resulting from the vegetative multiplication is small and rarely exceeds twenty-five. Usually the number of seeds per fruit is three or four, and quite frequently some of the flowers fail to set fruits. The average output is therefore probably between 12 and 15 seeds per plant.

Wood Anemone, *Anemone nemorosa* L.

The rhizomes of this species commonly bear but a single flower. The number of achenes was determined in forty-one fruiting heads, as shown in Table LXXXVIII. In the first column the number of mature and apparently

TABLE LXXXVIII. VARIATION IN NUMBER OF ACHENES PER PLANT OF *ANEMONE NEMOROSA*

| Number of carpels | Number of plants | Number of plants | Number of carpels | Number of plants | Number of plants |
|---|---|---|---|---|---|
| 9 | – | 1 | 25 | 2 | 5 |
| 11 | – | 1 | 26 | – | 1 |
| 13 | 1 | 4 | 27 | 4 | 7 |
| 14 | – | 3 | 28 | 1 | 3 |
| 15 | – | 8 | 29 | 3 | 2 |
| 16 | 1 | 9 | 30 | 4 | 3 |
| 17 | 1 | 8 | 31 | – | 3 |
| 18 | 3 | 12 | 32 | – | 1 |
| 19 | 2 | 14 | 33 | 1 | 6 |
| 20 | 3 | 5 | 36 | 1 | 2 |
| 21 | 5 | 16 | 37 | – | 1 |
| 22 | 4 | 10 | 39 | – | 1 |
| 23 | 3 | 15 | 41 | – | 1 |
| 24 | 1 | 10 | 42 | 1 | – |

fertile carpels borne by these forty-one plants is shown, and in the second column the data from 152 specimens as to the number of carpels. This second

set is taken from the author's paper on the trimery in the Ranunculaceous flower (Salisbury, E. J. (1919), *Ann. Bot.* XXXIII, No. CXXIX, pp. 47–79), and it may be noted that both the fertilized and unfertilized carpels show a preponderance of multiples of three. One would naturally expect the average for the number of mature achenes to be less than that obtained from the counts of immature carpels, some of which might well remain unfertilized, but actually the average number of mature carpels for the forty-two plants is 24·1, whilst for the 152 flowers the average number of carpels is 21·5. In both the most frequent number of carpels is twenty-one and the range is

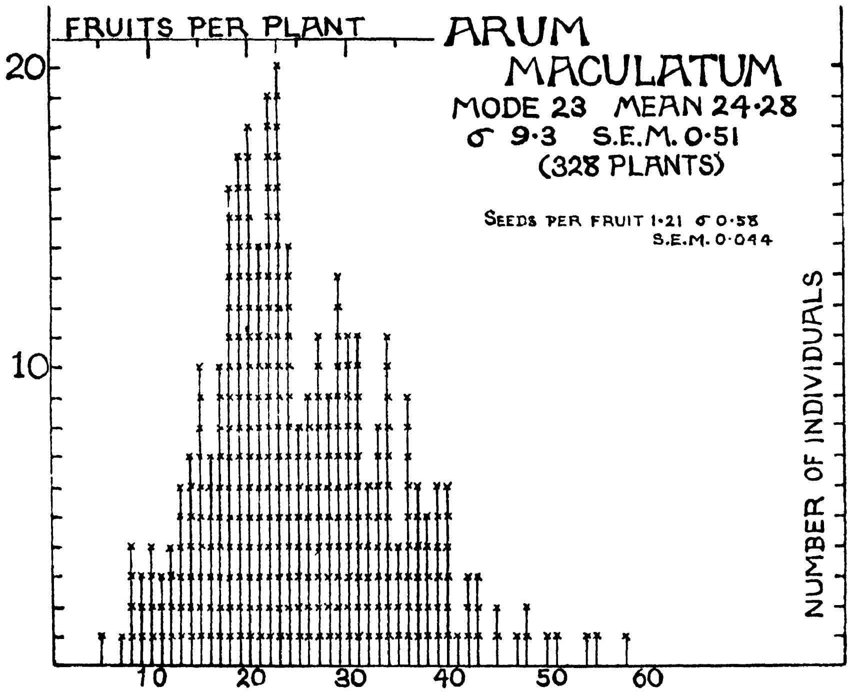



FIG. 28. Frequency distribution of the number of fruits on 382 plants of the Cuckoo-Pint (*Arum maculatum*).

almost the same. It would, then, appear probable that most of the carpels of *A. nemorosa* become fertile, and we shall be likely to gain rather than lose in the accuracy of our estimate if we treat the two sets of data collectively, as though both represented fertilized carpels. The average for 193 plants is then 22 carpels per plant (22·1±0·29; $\sigma$ 5·8; S.E.M. 0·44).

Cuckoo-Pint, *Arum maculatum* L.

Fruiting specimens of this species from Hertfordshire, Kent, and Pembrokeshire were examined, totalling 328 plants. The data are given in Table LXXXIX and shown graphically in Fig. 28. The mode is twenty-three and the arithmetic mean 24·28±0·34 ($\sigma$ 9·3; S.E.M. 0·51). An examination of one hundred and seventy-five fruits showed a range in the number of seeds from 1 to 4 (1 (150), 2 (16), 3 (6), 4 (3)), with 86 per cent of the fruits con-

TABLE LXXXIX. VARIATION IN NUMBER OF FRUITS PER PLANT OF *ARUM MACULATUM* L.

| Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals |
|---|---|---|---|---|---|---|---|
| 5 | 1 | 19 | 17 | 33 | 8 | 47 | 1 |
| 6 | 0 | 20 | 18 | 34 | 11 | 48 | 2 |
| 7 | 1 | 21 | 14 | 35 | 4 | 49 | 0 |
| 8 | 4 | 22 | 19 | 36 | 9 | 50 | 1 |
| 9 | 3 | 23 | 20 | 37 | 6 | 51 | 1 |
| 10 | 4 | 24 | 14 | 38 | 5 | 52 | 0 |
| 11 | 3 | 25 | 8 | 39 | 6 | 53 | 0 |
| 12 | 4 | 26 | 9 | 40 | 6 | 54 | 1 |
| 13 | 6 | 27 | 11 | 41 | 1 | 55 | 1 |
| 14 | 7 | 28 | 9 | 42 | 3 | 56 | 0 |
| 15 | 10 | 29 | 13 | 43 | 3 | 57 | 0 |
| 16 | 7 | 30 | 11 | 44 | 0 | 58 | 1 |
| 17 | 10 | 31 | 11 | 45 | 2 | | |
| 18 | 16 | 32 | 6 | 46 | 0 | | |

taining but a single seed. The average is 1·21±0·029 ($\sigma$ 0·58; S.E.M. 0·044). The average seed output of this species is therefore 29·4±1·1 seeds per plant. W. Wattam (1938, *Yorkshire Naturalist*, 977, p. 183) records that of forty seeds sown in April all germinated and formed corms. In one test made by the writer the germination was under 6 per cent, so it would appear that the viability is somewhat variable and the average reproductive capacity does not perhaps exceed 20 potential offspring per plant per annum.

Broad-leaved Garlic, *Allium ursinum* L.

The majority of the capsules of this species contain six seeds, and the number of capsules per plant was found to vary between six and thirty, with an average of 15·8. The mean seed output was 95±2·8 ($\sigma$ 36·6; S.E.M. 4·2). Germination averages about 70 per cent, so that the average reproductive capacity would be about 67±2 potential offspring per plant per annum.

Oxlip, *Primula elatior* Jacq.

Only twenty-eight specimens of this species were examined, and these yielded from 4 to 176 fruits per plant. The average was 17·07±3·5 ($\sigma$ 27·9; S.E.M. 5·2) fruits per plant. The seeds were counted in five mature average-sized capsules, and contained from 35 to 61 apparently fertile seeds. The average was 51±3 ($\sigma$ 10·0; S.E.M. 4·5). The average seed output from these data would then be 881±230 seeds per plant per annum.

Green Hellebore, *Helleborus viridis* L.

The number of fruits per plant on twenty-five specimens varied from two to seventy, the average number being 12·8±1·9 ($\sigma$ 14·3; S.E.M. 2·8). Each fruit usually consists of three follicles. The actual proportions of the various numbers of follicles per fruit were as follows: One follicle (6 per cent), two (19 per cent), three (44 per cent), four (28 per cent), five (3 per cent), an

average of $3{\cdot}0 \pm 0{\cdot}08$. The number of fertile seeds varied from one to nine in each follicle, with an average of $4{\cdot}9 \pm 0{\cdot}52$. Thus, the estimated average output of seeds per plant per annum would be $191 \pm 48$.

Mr. T. A. Dymes informs me that of three sets of seed of this species two failed to germinate whilst the third yielded 16 per cent germination. The reproductive capacity is therefore quite probably under 50 potential offspring per plant per annum.

Stinking Hellebore, *Helleborus foetidus* L.

Sixteen adult plants of this species were examined and yielded from 11 to 171 fruits. The average was $83{\cdot}6 \pm 7{\cdot}6$ ($\sigma$ 45·6; S.E.M. 11·4). Each fruit consists of from one to four follicles (one follicle (1 per cent), two (50 per cent), three (44 per cent), four (5 per cent), an average of $2{\cdot}43 \pm 0{\cdot}43$. The fertile seeds per follicle varied from two to fifteen, with an average of $9{\cdot}7 \pm 0{\cdot}48$ seeds. The average output of seeds per plant would therefore be $1{,}984 \pm 312$. Germination in this species is normally high, though exact data are not available. Seedling mortality is apparently low, and indeed in cultivation the plant is liable to become a pest, in marked contrast to the slow rate of increase of *H. viridis*. Hence the much higher output of *H. foetidus* cannot be regarded as compensatory for greater risks of non-survival.

Lungwort, *Pulmonaria longifolia* Boreau (*P. angustifolia* Auct. Angl. non L.)

Only a few specimens of this species have been examined, which indicated an average output of between 130 and 150 schizachenes per plant. Mr. B. T. Lowne records a germination of 69 per cent, and my own tests average 64 per cent, so we shall probably not be far wrong if we place the average reproductive capacity at about 90 potential offspring per plant per annum.

Wood-violet, *Viola sylvestris* Kit.

The capsules per plant average about eighteen, and the number of seeds in each ranged from 16 to 26 (average 22·5). The average seed output is therefore probably about 400 per plant.

Wood-rush, *Luzula pilosa* Willd.

The capsules produced by fifty plants of this species totalled 3,670, an average of $73{\cdot}4 \pm 6{\cdot}14$ fruits per plant. The number of capsules per plant ranged from 7 to 327 ($\sigma$ 63·83; S.E.M. 9·1). In a total of sixty-four capsules dissected, nineteen contained two seeds and forty-five contained three seeds, an average of $2{\cdot}7 \pm 0{\cdot}036$ ($\sigma$ 0·44; S.E.M. 0·055). The mean seed output is thus about $198 \pm 19$ seeds per plant per annum.

*Luzula Forsteri* DC.

The capsules of this species usually contain three seeds, and the number of capsules per plant was only determined for ten specimens, and ranged from 10 to 313. These would represent an average seed output of $233 \pm 52$. It is, however, doubtful whether this species normally produces more seeds than *L. pilosa*.

Stinking Iris, *Iris foetidissima* L.

The number of capsules per plant averages thirteen, and each contains an average of 28 seeds, so that the average seed output is about 364 seeds per plant. This species, it is interesting to note, is associated with two different types of habitat, namely woodlands on basic soils and on calcareous dunes of the west. In either habitat the large food reserve in the seed is advantageous.

Herb Paris, *Paris quadrifolia* L.

In Britain, fruit production of this species is usually sparse, and indeed in some localities it would appear to be almost entirely vegetative, spreading by means of its monopodial rhizomes. Hence, although a single fruit may produce 8 to 32 seeds, the average output per unit area is very low.

Solomon's Seal, *Polygonatum* species, and Lily-of-the-Valley, *Convallaria majalis* L.

As with *Paris*, the spread of these is mainly by rhizomatous growth, and the term " individual " has little meaning. Yet not only is the number of flowers per inflorescence small, but the proportion of these which set fruit is low, and in Britain large patches often fail to produce any seed whatever. On the Continent their fruit production would appear to be more prolific, but even there they would appear to agree with other woodland types in exhibiting a low output per unit area.

Snowdrop, *Galanthus nivalis* L.

This southern type is probably not native and its increase is largely vegetative. Each flowering bulb can only produce one fruit that, if fertile, contains usually from 12 to 18 seeds. It is evident that the seed output per unit area is low, and this is true also for the allied Snowflake, *Leucojum vernum.*

Pig-nut, *Conopodium denudatum* Koch.

This is a species which endures comparatively deep shade in the vegetative condition but only flowers freely when the light intensity is moderately high. As, however, it will colonize in moderate shade it is included in this category.

A total of 121 specimens were examined for fruit production, and the number of schizachenes per plant was found to range from 40 to nine hundred and fifty-eight. The average was $215{\cdot}5 \pm 9$. The distribution is shown in Table XC. Attention may be drawn to the contrast between these data and those furnished by Scott-Elliot (1932, *North Western Naturalist*, p. 183), who gives the average number of fruits per plant as only 28 (or 56 schizachenes) and the range as from 1 to 97, compared with the 20 to 479 here observed. The average of $215 \pm 9$ ($\sigma$ 149; S.E.M. 13·5) is considerably in excess of the modal value, which would appear to be about 50 fruits or less.

Wood Spurge, *Euphorbia amygdaloides* L.

This plant can be regarded as a shade species in the sense that established individuals will persist for a number of years in situations of low light intensity, but in such it is often entirely vegetative, even if flowers are formed. The only data available are for the number of female flowers on sixteen plants, including

TABLE XC. VARIATION IN NUMBER OF SCHIZACHENES PER PLANT OF *CONOPODIUM DENUDATUM*

| Schizachenes per plant | Number of individuals | Schizachenes per plant | Number of individuals | Schizachenes per plant | Number of individuals | Schizachenes per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 40 | 1 | 106 | 1 | 202 | 1 | 356 | 1 |
| 46 | 1 | 108 | 3 | 204 | 1 | 370 | 1 |
| 52 | 1 | 114 | 2 | 206 | 1 | 372 | 1 |
| 56 | 1 | 116 | 1 | 216 | 1 | 376 | 1 |
| 58 | 1 | 118 | 1 | 226 | 1 | 380 | 1 |
| 62 | 1 | 120 | 4 | 230 | 1 | 382 | 1 |
| 64 | 1 | 122 | 1 | 242 | 1 | 384 | 1 |
| 68 | 2 | 128 | 2 | 260 | 1 | 394 | 1 |
| 70 | 1 | 134 | 1 | 268 | 1 | 396 | 1 |
| 72 | 2 | 140 | 1 | 270 | 2 | 398 | 1 |
| 74 | 2 | 142 | 1 | 276 | 1 | 410 | 1 |
| 76 | 2 | 144 | 2 | 280 | 1 | 412 | 1 |
| 80 | 2 | 154 | 1 | 284 | 1 | 426 | 1 |
| 82 | 2 | 158 | 1 | 312 | 1 | 432 | 2 |
| 84 | 1 | 164 | 1 | 314 | 1 | 434 | 1 |
| 88 | 1 | 168 | 1 | 318 | 1 | 436 | 1 |
| 90 | 2 | 170 | 1 | 322 | 2 | 438 | 1 |
| 92 | 2 | 176 | 1 | 326 | 1 | 492 | 1 |
| 94 | 2 | 178 | 1 | 328 | 1 | 506 | 1 |
| 96 | 2 | 184 | 1 | 330 | 2 | 510 | 1 |
| 98 | 2 | 186 | 1 | 338 | 1 | 612 | 1 |
| 100 | 2 | 192 | 2 | 346 | 2 | 958 | 1 |
| 102 | 2 | 194 | 1 | 352 | 1 | | |
| 104 | 1 | 200 | 1 | 354 | 1 | | |

Total of 26,080 schizachenes on 121 plants.

some large individuals growing in light patches and coppiced areas. These plants bore from 27 to 690 female flowers with an average of 230$\pm$39 ($\sigma$ 237; S.E.M. 59). It is probable that the average for a much larger and more representative population sample would be appreciably lower. A considerable proportion of the female flowers may not set seed, but even assuming that all the female flowers formed fruits and that most contained the full complement of three seeds, the total average output would be 690 seeds under the favourable conditions in which these plants were growing. The seeds germinate in June, and the seedlings are often numerous in coppiced areas.

Lesser Periwinkle, *Vinca minor* L.

This is an example of a species that rarely produces seed in this country, although it often flowers profusely in woodland areas that have been coppiced. It spreads rapidly by means of its runners, and fruit production is encouraged if these be removed. Even then, however, fruit formation is sparse and, as each fruit produces only from 1 to 4 seeds, the total output is very low.

Ladies Smock, *Cardamine pratensis* L.

In the damp calcareous woodlands of Kent *Cardamine pratensis* is often an abundant constituent of the woodland flora. Although flowering profusely,

here as in many damp meadows, the seed production is frequently small. White (1912), writing of this species in the "Flora of Bristol," mentions that it frequently does not perfect its seed pods, and that 70 per cent of the plants in damp habitats may reproduce vegetatively by means of buds at the base of the terminal leaflets. In some other Cruciferous woodland plants such as the Coral-root, *Dentaria bulbifera*, and the Wood Cress, *Nasturtium sylvestre*, which also reproduce vegetatively, the formation of fertile seeds is the exception.

Yellow Dead-nettle, *Galeobdolon luteum* Huds.

The inclusion of this species here is perhaps scarcely justified, since its flowering and fruiting is so dependent upon a comparatively high light intensity. In the deeper shade this species can persist, and may even spread appreciably by means of its runners, but it remains sterile until the woodland is coppiced or the light intensity is otherwise increased. Owing to its rapid vegetative spread, however, it is not, like the species of intermittently open habitats, restricted as to the extension of its area of occupation to the periods when the light intensity is high and competition greatly diminished.

The average output for the plants examined was $797 \pm 161$, or approximately between 640 and 960 seeds per plant. The largest output for any one plant was 5,628 schizachenes.

Enchanter's Nightshade, *Circaea lutetiana* L.

Although this species is often abundant in coppiced areas and light gaps in woodlands its presence in quite shady areas of the Fagetum, of which community it is a characteristic species, and its ability to colonize from seed in such justifies its inclusion here. The data from ninety-six plants were obtained from Beech-woods on chalk (Table XCI).

TABLE XCI. VARIATION IN NUMBER OF FRUITS PER PLANT OF *CIRCAEA LUTETIANA* L.

| Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals |
|---|---|---|---|---|---|---|---|
| 11 | 2 | 33 | 3 | 64 | 2 | 118 | 1 |
| 13 | 2 | 34 | 4 | 69 | 1 | 120 | 1 |
| 15 | 3 | 35 | 1 | 71 | 1 | 129 | 1 |
| 16 | 2 | 38 | 1 | 72 | 1 | 132 | 1 |
| 18 | 1 | 40 | 4 | 77 | 1 | 137 | 1 |
| 19 | 4 | 43 | 3 | 80 | 1 | 138 | 1 |
| 20 | 5 | 46 | 2 | 81 | 1 | 139 | 1 |
| 23 | 1 | 48 | 1 | 82 | 1 | 175 | 1 |
| 24 | 3 | 50 | 2 | 85 | 1 | 195 | 1 |
| 25 | 3 | 52 | 2 | 90 | 1 | 206 | 1 |
| 26 | 1 | 54 | 1 | 92 | 2 | 237 | 1 |
| 27 | 3 | 56 | 1 | 93 | 2 | 276 | 1 |
| 28 | 1 | 60 | 1 | 95 | 1 | 347 | 1 |
| 29 | 1 | 61 | 1 | 106 | 1 | | |
| 30 | 1 | 62 | 1 | 109 | 1 | | |
| 31 | 1 | 63 | 1 | 110 | 1 | | |

Total of 5,952 fruits on 96 plants.

The average number of fruits per plant was $62 \pm 3{\cdot}9$ ($\sigma$ 58·3; S.E.M. 5·8). The fruit, though containing two seeds, is indehiscent and effectively dispersed through being covered with minute hooked hairs. Its congener, *C. alpina*, which is perhaps even more of a shade species, produces a smaller number of fruits, which are one-seeded and less efficiently dispersed. Both are pseudo-annuals, spreading vegetatively by means of stolons, which may attain a length of 30 cm. From two to six stolons are formed at the base of the flowering axis, the death of which brings about their separation. These in turn form flowering axes and basal stolons, so that there is potentially a geometrical progression of separated units. Thus, as in a number of other woodland species, the vegetative propagation is much the more important, especially as the " individual " thus produced has a much larger food reserve than is furnished by the seed.

*Trientalis europaea* L.

Like *Circaea*, this species is a pseudo-annual type, with fewer stolons, but each with a swollen sub-terminal region constituting the food reserve. The stolon produces a single inflorescence bearing from one to four flowers. The average number of fruits per plant is two, and each capsule contains from 1–6 seeds, with an average of $3{\cdot}4 \pm 0{\cdot}29$. The average seed output is therefore seven seeds per plant, and even an exceptionally vigorous plant will not produce more than twenty-four.

Germination, according to Kinzel, is 37 per cent in the dark and 70 per cent in the light. The latter figure would give an average reproductive capacity from seed of approximately five. The number of stolons is usually from 1 to 4, so that reproduction by both methods is very small in comparison with most species.

In view of the low seed output of these shade species it is of interest to note that the two woodland crucifers *Dentaria bulbifera* and *Nasturtium sylvestre*, though both flowering freely, rarely produce fertile seed. The former reproduces by means of axillary bulbils in the lower part of the inflorescence, whilst the former spreads by runners. The Solomon's Seals (*Polygonatum* species) are in general characterized by poor fruit production, and this is true also of *Convallaria majalis*, though in some seasons fruits are produced freely and the seeds have good viability (64 to 98 per cent); but rarely is the seed output anything but small, and the reproduction is mainly vegetative, especially in the northern parts of their range. This is probably true also of *Paris quadrifolia*, the seed output of which is certainly small.

Lesser Celandine, *Ficaria verna* (*Ranunculus Ficaria* L.)

This species occurs, as pointed out by Marsden-Jones (1935), in two varieties: the one reproducing by seed, which is a diploid, and the other, which is a tetraploid, mainly by bulbils and rarely by seed (*var. bulbifera* Marsden-Jones). In the paper cited data are furnished for the seed production of twenty plants of the diploid strain, of which ten were sun-plants and ten others shade-plants; but as the average seed production was much the same in both situations, viz. 75 and 71 seeds per plant, the data have been treated

together. The range is from 4 to 146 of apparently viable achenes per plant. The standard deviation calculated for the twenty individuals is 39·3 and the standard error 8·7. The average is thus 73±5·8 apparently viable achenes per plant. Marsden-Jones obtained 71 per cent germination with one hundred achenes, and if this be representative would indicate a reproductive capacity of about fifty-two. Sixty achenes of *v. bulbifera* yielded only 15 per cent germination. H. Woltner (1933) made tests on far larger numbers and obtained an average of 50 per cent germination, on which basis the reproductive capacity would be only about 36 potential offspring per plant. This investigator showed that the germination, which takes place in from 11–23 weeks, is independent of light.

TABLE XCII. SUMMARY OF REPRODUCTION RATES OF SHADE SPECIES

| Species | Average seed output | Average weight of seed per plant in grams |
|---|---|---|
| Trientalis europea | 7 | |
| Adoxa moschatellina | *ca.* 14 | 0·00994 |
| Mercurialis perennis | *ca.* 15 | 0·1185 |
| Galanthus nivalis | *ca.* 15 | |
| Paris quadrifolia | *ca.* 20 | 0·09 |
| Anemone nemorosa | 22·1±0·29 | |
| Arum maculatum | 29·4±1·1 | 1·3336 |
| Circaea lutetiana | 62±3·9 | |
| Ficaria verna | 73±5·8 | |
| Scilla nutans | 91±4·0 | 0·5369 |
| Allium ursinum | 95±2·8 | 0·6998 |
| Pulmonaria longifolia | *ca.* 140 | 1·45 |
| Helleborus viridis | 191±48 | *ca.* 2·2 |
| Luzula pilosa | 198±19 | |
| Luzula Forsteri | *ca.* 233±52 | *ca.* 0·21 |
| Conopodium denudatum | 215±9 | |
| Iris foetidissima | *ca.* 364 | *ca.* 17·4 |
| Viola sylvestris | *ca.* 400 | |
| Ornithogalum pyrenaicum | *ca.* 400 | 4·3 |
| Galeobdolon luteum | 797±161 | 2·125 |
| Primula elatior | 881±230 | 0·794 |
| Helleborus foetidus | 1,984±312 | *ca.* 17·5 |

Mean of averages for twenty-two species 280 seeds per plant. Average weight 2·2 gm./pl.

Though some of these determinations are very approximate it is obvious that, even allowing a considerable margin of error for the mean of 291 seeds per plant, the seed output of these shade species is much lower than for species of closed but well illuminated habitats, and, indeed, the species of (a) open habitats, (b) semi-closed communities, (c) closed but not shady communities, and (d) shady communities, present a descending series in this respect.

It can, however, be urged with justice that some of the above species which are markedly social in habit should have their productivity estimated upon a basis of unit area. Such a basis would be appropriate for *Adoxa moschatellina, Mercurialis perennis, Anemone nemorosa, Scilla nutans*, and *Allium ursinum.* A dense growth of the first, flowering freely, will produce about nine inflores-

cences in 100 sq. cm., or 126 seeds per sq. dm., but the average density of the fruit heads was 0·7 per sq. dm. Again, in coppiced areas, where flowering of *Anemone nemorosa* is most prolific, an exceptionally floriferous area occupied by this species showed an average density of 380 flowers per sq. m., but the average number of fruiting heads in woodland with sparse shrubs in almost pure societies of this species was 152 per sq. m., which would imply an output of about 33 achenes per sq. dm. The number of inflorescences in the same area of a wood with a denser shrub layer is, however, much less and the seed output proportionally smaller. Since plants of *Mercurialis perennis* normally occupy more than a decimetre in area the figure for this species would be lower on an area basis. Only for *Scilla nutans* and *Allium ursinum* would this mode of computation yield appreciably higher figures for the seed output. For the former the yield per sq. dm. in a dense and freely-flowering community of this species would be about 500 seeds.[1]

It will then be evident that, whatever the basis of computation, the seed production of the shade flora species does not attain to anything like the output met with in most of the species of the other types of habitat considered.

## Species of Intermittently Open Habitats

The species characteristic of the marginal flora of woodlands belong in part to this category, although others of the marginal flora are restricted thereto. The types we are here concerned with find, it is true, a more frequently available home in the better-lighted spots at the edge of woods and in scrub, but their chief development is in the light gaps, whether these be small, as from the fall of a moribund tree, or large, as from coppicing or felling of an extensive area. Fires also often provide the requisite conditions.

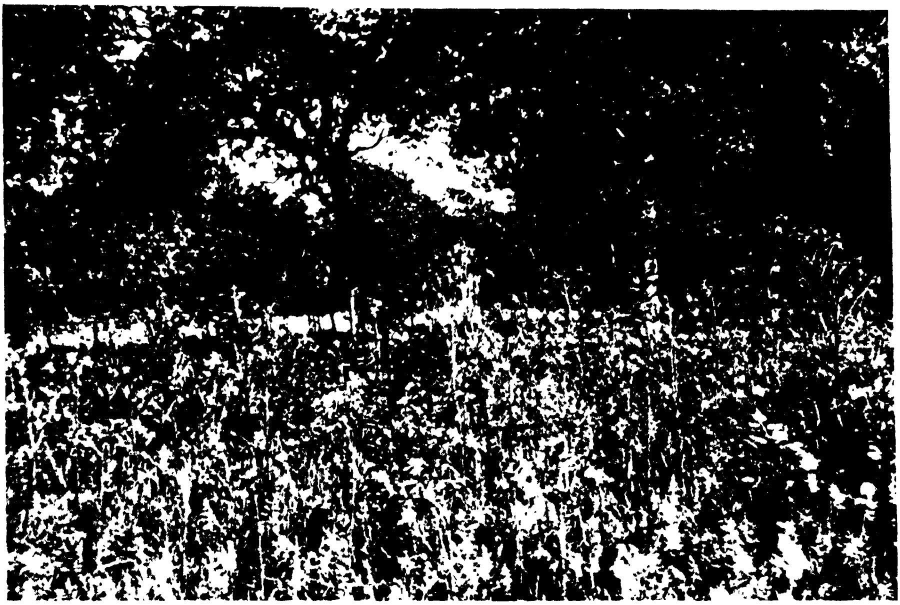
Of such woodland types characteristic of intermittently open habitats the following species are examples: *Barbarea vulgaris*, *Cirsium palustre*, *Digitalis purpurea*, *Dipsacus sylvestris*, *Dipsacus pilosus*, *Epilobium angustifolium*, *Epilobium montanum*, *Epilobium tetragonum*, *Galeopsis tetrahit*, *Gnaphalium sylvaticum*, *Hypericum hirsutum*, *Hypericum perforatum*, *Lychnis dioica*, *Scrophularia nodosa*, *Senecio sylvaticus*, *Verbascum Thapsus*, and *Verbascum Lychnitis*. Of these seventeen species all are common features of coppiced areas, with the exception of *Dipsacus pilosus* and *Verbascum Lychnitis;* but even these, rare though they be, share with the other species the characteristic of sometimes occupying such areas in amazing abundance, almost certainly due in certain instances, and to some extent perhaps in all, to the presence of dormant seeds in the woodland soils.

### Wood-rush, *Luzula multiflora* DC.

The capsules counted on twenty-six plants of this species totalled 10,796, and the individual production ranged from 90 to 6,534 seeds per plant per

[1] Even for the shade tolerant *Scilla nutans* the number of inflorescences produced is greater in the better illuminated parts of the wood, and the writer has elsewhere furnished data that show a diminution of the number of flowers per inflorescence of this species in the uncut wood as compared with inflorescences in coppiced areas, a diminution that amounted to from 19 to 24 per cent (*cf.* E. J. Salisbury, 1924, "The Effects of Coppicing as illustrated by the Woods of Hertfordshire," *Trans. Herts. Nat. Hist. Soc.*, XVIII, pp. 1–21).

PLATE III



Marsh Thistles (*Cirsium palustre* (L.) Scop.) in wood 2nd year after coppicing.

Mulleins (*Verbascum Thapsus* L.) in coppiced woodland, density 5·2 per square metre.

annum. The average was $1{,}245 \pm 208$ seeds per plant ($\sigma$ 1,577; S.E.M. 309) or, in round figures, between one thousand and fourteen hundred and fifty.

The average weight of a seed is 0·000418 gm., so that the weight of seeds per plant has a mean value of between 0·43 and 0·6 gm.

Foxglove, *Digitalis purpurea*

The capsule production was determined for one hundred and two plants, and ranged from 15 to 428 per plant. The average number of capsules was $83 \pm 4$ ($\sigma$ 62·3; S.E.M. 6·1) or a mean of between 79 and 87 capsules per plant.

The number of seeds per capsule was determined for 26 fruits, and ranged from 363 to one thousand three hundred and seventy-nine. The average number of seeds per capsule was $1{,}029 \pm 36$ ($\sigma$ 271; S.E.M. 54).

The mean seed output for *Digitalis purpurea* from these data is $85{,}551 \pm 7{,}104$ seeds per plant, or approximately between 78,000 and 93,000 seeds per plant. The germination of Foxglove seeds in light is usually high (Kinzel obtained 100 per cent and Nobbe and Hanlein 97 per cent),[1] and the average is probably over 95 per cent, so that the average reproductive capacity probably exceeds 81,000 potential offspring per plant. *D. purpurea* is usually biennial or triennial, though specimens occasionally fruit a third or even a fourth year. It might therefore not inappropriately be termed a very short-lived perennial.

This species affords an illustration, in a striking degree, of fluctuation in population number. Usually sparsely present at the woodland margin as scattered individuals, I have seen an area of many acres in extent in a valley near Knighton, where, in the second year after coppicing, the whole was occupied by an almost continuous array of flowering plants of this species, averaging about twelve to the square metre. Vast as is the seed output of a single individual, this complete carpeting of the ground could scarcely be due to seeding from the marginal specimens alone, present before the woodland was cut. One must presume the germination of seeds, dormant in or beneath the litter, stimulated into activity by the access of light and probably also by the reduction in the $CO_2$ concentration of the soil atmosphere. But, be this as it may, the salient feature is the change from a marginal population measured in hundreds, and more or less stable over a period of years, giving place for a brief interval to a population measured in millions (*cf.* Frontispiece).

Teazel, *Dipsacus sylvestris* Huds.

The number of fruiting heads per plant of the Teazel were counted on 270 specimens, and varied from a single head to twenty-five, as follows: 1 (110), 2 (10), 3 (53), 4 (15), 5 (23), 6 (14), 7 (12), 8 (1), 9 (8), 10 (4), 11 (4), 12 (3), 13 (3), 14 (2), 15 (2), 19 (1), 20 (1), 21 (1), 22 (1), 24 (1), 25 (1). A total of 1,060, or an average of $3{\cdot}9 \pm 0{\cdot}17$ heads per plant ($\sigma$ 4·14; S.E.M. 0·25).

The number of fruits in thirteen fruit-heads was as follows: 382, 454, 495, 500, 515, 543, 650, 756, 768, 890, 952, 1,034, 1,892; a total of 9,831 fruits, or an average of $756 \pm 70{\cdot}9$ achenes per fruiting head ($\sigma$ 382·7; S.E.M. 106·3). The average seed output was therefore $2{,}960 \pm 405$ per plant. It will be noted that the most frequent number of fruit-heads per plant is one, and large

[1] *Landw. Versuchs.*, 6 Stat. XX, 63, 1877.

populations normally exhibit a high proportion of small individuals and a small number of very large ones. In our random sample nearly one-third of the fruiting heads were produced by plants with ten or more and about 27 per cent by plants with three or less.

Shepherd's Rod, *Dipsacus pilosus* L.

The individual heads of this species bear from 40 to 90 fruits, with an average of 64·8±1·8 achenes.

The number of fruit-heads per plant shows a wide range. The smallest specimens examined bore only ten such, whilst the largest produced six hundred. The average was 180±47 fruiting heads, so that the average output would be 11,749±3,370 achenes per plant, or approximately between eight thousand and fifteen thousand.

Rose-bay Willowherb, *Epilobium angustifolium* L.

Only a small number of plants and capsules of this species have been examined, but the number of seeds per capsule would appear to range from about 250 to 500, with an average of about 380 seeds, whilst a relatively small plant will produce some 200 capsules. The average output of seeds is therefore at least of the order of 76,000 seeds per plant per annum. In addition *E. angustifolium* spreads vegetatively at a rapid rate. Experiments carried out by A. Niethammer (1927) with seeds of this species show them to require light for their germination but to lose the need for the light stimulus with storage. *E. parviflorum* was found to retain the need for light after prolonged storage.

Willowherb, *Epilobium montanum* L.

A total of 178 plants of this species were examined for capsule production, which ranged from 1 to 155 per plant (Table XCIII). The average is

TABLE XCIII. VARIATION IN NUMBER OF CAPSULES PER PLANT OF *EPILOBIUM MONTANUM* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 15 | 4 | 29 | 4 | 64 | 1 |
| 2 | 3 | 16 | 4 | 31 | 2 | 73 | 1 |
| 3 | 3 | 17 | 3 | 32 | 3 | 74 | 2 |
| 4 | 10 | 18 | 5 | 33 | 2 | 80 | 1 |
| 5 | 9 | 19 | 2 | 37 | 3 | 83 | 1 |
| 6 | 6 | 20 | 9 | 38 | 1 | 86 | 2 |
| 7 | 7 | 21 | 1 | 39 | 4 | 88 | 1 |
| 8 | 13 | 22 | 1 | 40 | 1 | 101 | 1 |
| 9 | 6 | 23 | 5 | 41 | 1 | 103 | 1 |
| 10 | 13 | 24 | 2 | 45 | 1 | 125 | 1 |
| 11 | 10 | 25 | 2 | 47 | 1 | 155 | 1 |
| 12 | 7 | 26 | 1 | 55 | 1 | | |
| 13 | 4 | 27 | 1 | 59 | 1 | | |
| 14 | 3 | 28 | 3 | 60 | 2 | | |

Total of 3,802 capsules on 178 plants.

$21 \pm 1{\cdot}1$ ($\sigma$ 23·8; S.E.M. 1·7). The seeds were counted in forty-five capsules. The numbers were as follows: 38, 46, 60, 67, 68, 71, 78, 80, 84 (2), 93, 94, 99 (2), 100, 104, 105, 109, 110, 111 (2), 112, 120, 122 (2), 123 (2), 125, 126, 130 (2), 134, 135, 146, 147, 151 (2), 162 (2), 163, 172, 179, 182, 187, 190, a total of 5,305 seeds, or an average of $117{\cdot}9 \pm 3{\cdot}7$ ($\sigma$ 37; S.E.M. 5·5). Although the data for numbers of seeds per capsule are insufficient to display a definite mode they suggest by their aggregation a mode between 110 and one hundred and thirty.

From the data furnished the average seed output would be $2{,}480 \pm 207$ seeds per plant per annum. Germination tests indicate an average of about 94 per cent, giving a reproductive capacity of 2,331 potential offspring per plant per annum.

Willow-herb, *Epilobium tetragonum* L.

One hundred and sixty-four plants of this species were examined for capsule production and showed a range of from five to 277 capsules per plant. As shown in Table XCIV, there is no obvious mode, but a suggestion of such between 30 and 40 capsules. The average is 47 ($47{\cdot}3 \pm 3{\cdot}2$; $\sigma$ 44·7; S.E.M. 3·4).

TABLE XCIV. VARIATION IN THE NUMBER OF CAPSULES PER PLANT OF *EPILOBIUM TETRAGONUM* L.

| Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals | Capsules per plant | Number of individuals |
|---|---|---|---|---|---|---|---|
| 5 | 1 | 27 | 1 | 50 | 1 | 92 | 1 |
| 6 | 1 | 28 | 3 | 51 | 1 | 93 | 1 |
| 8 | 1 | 29 | 3 | 52 | 1 | 94 | 2 |
| 9 | 6 | 30 | 3 | 54 | 2 | 97 | 1 |
| 10 | 1 | 31 | 3 | 56 | 1 | 101 | 1 |
| 11 | 2 | 32 | 4 | 57 | 1 | 104 | 1 |
| 12 | 1 | 33 | 3 | 59 | 1 | 110 | 1 |
| 13 | 6 | 34 | 6 | 63 | 1 | 112 | 1 |
| 14 | 2 | 35 | 4 | 64 | 1 | 121 | 1 |
| 15 | 5 | 37 | 3 | 65 | 2 | 123 | 1 |
| 16 | 4 | 38 | 2 | 67 | 2 | 124 | 1 |
| 17 | 2 | 39 | 6 | 69 | 1 | 156 | 1 |
| 18 | 3 | 40 | 5 | 71 | 1 | 171 | 1 |
| 20 | 5 | 41 | 1 | 80 | 2 | 177 | 1 |
| 21 | 4 | 42 | 1 | 81 | 1 | 185 | 1 |
| 22 | 3 | 43 | 3 | 83 | 1 | 186 | 1 |
| 23 | 1 | 45 | 4 | 84 | 1 | 217 | 1 |
| 24 | 4 | 46 | 3 | 86 | 1 | 260 | 1 |
| 25 | 2 | 47 | 1 | 88 | 1 | 277 | 1 |
| 26 | 4 | 48 | 3 | 89 | 1 | | |

Total of 7,797 capsules or 164 plants. Average $47{\cdot}3 \pm 3{\cdot}2$.

The seeds were counted in forty-five capsules, and ranged in number from 65 to 225, as follows: 65, 83, 85, 101, 104, 105, 112, 118, 126, 135, 144, 147, 148, 154, 155, 157, 158, 159, 161 (2), 162, 163 (2), 172, 174, 176, 178 (2), 179, 183, 190 (2), 191, 193 (2), 194, 195 (2), 198, 202, 213, 219 (2), 224, 225.

Total 6,869 seeds in 45 capsules. The average is 153 (152·6±3·9; $\sigma$ 39·8; S.E.M. 5·9). The average seed output is therefore 7,230±673 seeds per plant per annum. Only one germination test was carried out and this yielded 89 per cent germination, so that if this be typical the reproductive capacity would have an average value of about 6,435 potential offspring per plant per annum.

This species, like the preceding one, spreads vegetatively by means of stolons, but those of *E. tetragonum* are appreciably longer than those of *E. montanum*, so that whereas the offsets of the latter cluster round the parent rosette those of the former may be several centimetres distant.

Hemp-nettle, *Galeopsis tetrahit* L.

This self-fertile and autogamous species sometimes occurs in large numbers upon woodland clearings and coppiced areas. The schizachenes produced have only been counted upon sixteen specimens. The number of achenes ranged from 278 to 9,312; the average was 2,010 per plant ±384. Perhaps, then, as a rough approximation we may take the average output to be about 2,000. The only datum as to germination available is that of 36 per cent recorded by Kempski. If representative, this would imply a reproductive capacity of about 720; but field observations suggest that Kempski's figure may well be below the average.

Wood Cudweed, *Gnaphalium sylvaticum* L.

The numbers of fruiting capitula on forty-one plants were as follows: 23, 31, 37, 39, 42, 47, 48, 49 (2), 54, 56, 57, 59, 62, 64, 76, 78, 91, 92 (2), 95, 97, 98, 120, 121, 126, 130, 131, 138, 142, 171, 191, 193, 194, 224, 247, 259, 288, 343, 400, 571, a total of 5,465 fruiting heads, or an average of 132·3±11·4 ($\sigma$ 109·8; S.E.M. 17·1).

The number of fruits per capitulum was counted in twenty-six fruiting heads. Eklund gives data for a further ten heads which have been also utilized, so that the mean is based upon 36 counts, which are as follows: 33, 54 (2), 55 (2), 56, 57 (2), 58 (2), 60, 61, 64 (2), 65 (2), 66, 67 (4), 68, 70 (3), 71, 73, 74 (2), 75, 76, 86, 93, 96, 102, 106. For the thirty-six heads the total is 2,464 achenes, or an average of 68 (68·2±1·6; $\sigma$ 14·2; S.E.M. 2·36).

The average seed output would thus appear to be 9,042±991, or approximately between 8,050 and 10,000 achenes per plant per annum. This would represent a fruit weight of about 0·23 gm. per plant.

Red Campion, *Lychnis dioica* Mill.

Fifty-three specimens of this species were examined for capsule production, which ranged from 11 to 122 capsules per plant. The average was 33·3±1·8. As, however, all the specimens were obtained during a rather unfavourable year for this species it is probable that this average is a conservative one. The number of seeds in each capsule may be as few as 41 or as many as two hundred and eighty-eight. Guppy (1912, "Studies in Seeds and Fruits," p. 365) gives 250 as the average number of seeds per capsule and 300 as the average number of ovules. My own counts suggest a somewhat lower figure,

and probably 215±22 seeds per capsule would represent a more general average. These data indicate an average output of 7,193±1,124 seeds per plant, or roughly between six thousand and eight thousand seeds; but this is probably a conservative estimate, since medium-sized plants can produce up to 30,000 seeds.

Ploughman's Spikenard, *Inula Conyza* D.C. (*Inula squarrosa* (L.) Bernh.)

The Ploughman's Spikenard (*Inula Conyza*) is a biennial, which passes the vegetative period as a rosette plant, and as such is intolerant of surrounding herbage. It is found as a marginal species in the woodland flora, but is particularly a feature of coppiced areas, erosion slopes, and similar habitats that are only periodically available, so that, though it does occur in situations of a more permanent character, as, for instance, on the constantly disturbed soil near rabbit burrows on chalk, it may appropriately be considered here.

The number of capitula was counted on only ten plants but ranged from 73 to 1,960, the average being 521±130 ($\sigma$ 604·2; S.E.M. 195) capitula per plant. The achenes were counted in eighteen capitula and the numbers were as follows: 54, 59, 64, 71, 72, 77, 80, 82, 84, 87, 87, 92, 93, 102, 118, 120, 122, 160. A total of 1,634 achenes, or an average of 90±4 per capitulum. From these data, then, the average output would be 47,010±4,781, or approximately between 42,000 and 52,000 achenes per plant. Although the data are too few to obtain a reliable average, it is evident that the seed output is of the same order of magnitude as that of typical species of intermittently available habitats.

Golden Rod, *Solidago virgaurea* L.

This is probably more shade-enduring than the preceding species, but is, I believe, only capable of colonizing relatively well-illuminated locations. It is a characteristic plant of woodland clearings, and its occurrence in shaded woodland situations is probably to be accounted for by persistence in a diminishing light intensity subsequent to the relatively high intensity when colonization took place.

The number of achenes in the capitulum was determined in 178 fruiting capitula (*cf.* Fig. 29). The range was from nine fruits to thirty-five. The actual numbers were as follows: 9 achenes (1), 10 (4), 12 (5), 13 (9), 14 (13), 15 (18), 16 (27), 17 (19), 18 (20), 19 (15), 20 (15), 21 (5), 22 (10), 23 (8), 24 (1), 25 (3), 26 (1), 30 (1), 31 (2), 35 (1). The average is 21·4±0·27 ($\sigma$ 5·4; S.E.M. 0·4). The number of capitula per plant was determined for only a few specimens, the average of which was 192±60, so that the average number of achenes per plant was probably about four thousand.

Eklund gives the number of capitula on a small and large plant as 47 and 419 respectively, which would suggest a rather higher mean than our data.

Deadly Nightshade, *Atropa Belladonna* L.

The Deadly Nightshade (*Atropa Belladonna*) is a species which is found chiefly at wood margins and in clearings of beech woods on chalk. It is perhaps open to question whether it should be regarded as characteristically a colonizer of periodically available habitats or not, but the occurrence of

its seedlings suggests that it may be appropriately considered here. The fruits were counted on nine specimens only, of which the least prolific were growing in competition with dense vegetation and the largest were in open scrub. The numbers of fruits were as follows: 46, 202, 221, 292, 450, 517, 560, 785, 1,184, a total of 4,257 fruits or an average of 473±73 fruits per plant ($\sigma$ 327; S.E.M. 109).

The seeds were counted in twenty fruits (73, 113, 132, 137, 140, 142, 149, 150, 151, 154, 156, 159, 160, 161, 163, 170, 175, 191, 214, 221), yielding a

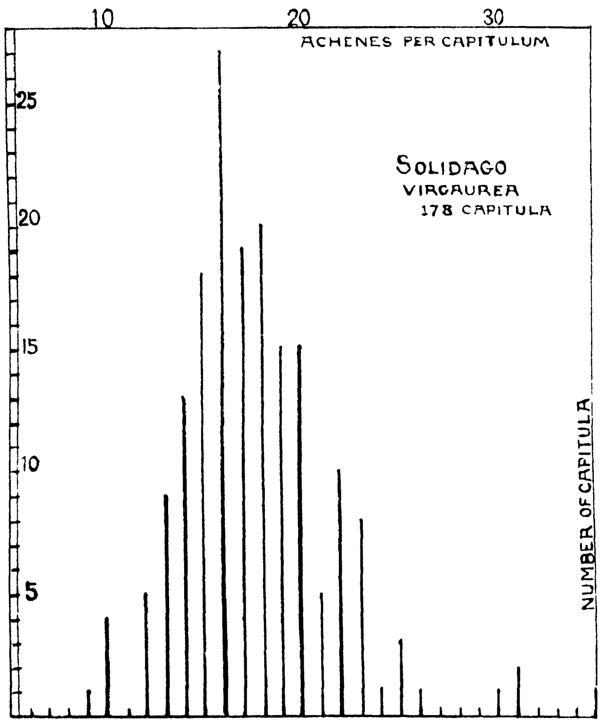



FIG. 29. Diagram showing the variation in number of achenes per capitulum of the Golden Rod (*Solidago virgaurea*). Ordinates represent the number of capitula and abscissae the number of achenes in the capitula.

total of 3,111 seeds, or an average of 155·5±4·7 ($\sigma$ 31·3; S.E.M. 7·1). The average seed output per plant would thus be 74,045±13,725 seeds per plant per annum. The average germination is about 60 per cent, so that the average reproductive capacity would be about 43,000 potential offspring each year. As the seeds are mainly distributed in bird droppings, the contents of each berry are often deposited together, and usually near some bush that serves as a convenient perch. Thus the dispersal is far more localized than might be expected, and wood margins, old chalk-pits, etc., where there are bushes, are far more frequently colonized than open chalkland where bushes are usually sparse.

Wood Groundsel, *Senecio sylvaticus* L.

This is a winter annual whose seeds germinate, often in great profusion, in the autumn. That the extensive carpets of this species which sometimes cover burnt areas on heaths are due to the presence of dormant seeds is suggested by the fact that multitudes of seedlings of this species have been observed by the writer on burnt areas in the autumn, although these same areas until a few months previous, when the fires occurred, had been covered for a period of years by dense thickets of Gorse, *Ulex europaeus*.

The number of capitula was counted on sixty-six plants from burnt heaths, and ranged from four to eight hundred and seven. These sixty-six plants bore a total of 15,942 fruiting capitula, or an average of $242 \pm 15{\cdot}6$ ($\sigma$ 190; S.E.M. 23·4). The number of achenes was determined in thirty-six fruit-heads, and varied as follows: 6 (1), 15 (1), 20 (1), 23 (1), 27 (1), 28 (2), 31 (2), 32 (1), 37 (3), 41 (3), 42 (1), 45 (1), 46 (1), 50 (3), 51 (1), 52 (3), 55 (2), 57 (2), 58 (1), 60 (1), 63 (2), 65 (1), 66 (1), a total of 1,564 fruits, or an average of $43{\cdot}4 \pm 1{\cdot}6$ ($\sigma$ 14·7; S.E.M. 2·4). The average fruit output is thus $10{,}638 \pm 954$ per plant. The output of some apparently average specimens taken from a coppiced woodland area was between 18,000 and 22,000, but, as we have already pointed out, this method of estimation is liable to give too high values; nevertheless it is probably true that the yield in such locations is at least as great, if not greater, than that of specimens from the heaths upon which our estimate was based.

Marsh Thistle, *Cirsium palustre* (L.) Scop.

This thistle of wet meadows and woods is a biennial that is particularly characteristic of coppiced areas and similar intermittently available habitats where the rosette stage of the first season can develop and persist in a relatively unshaded condition. In the second summer after coppicing the inflorescences of this species may be very common (*cf.* Plate III, which shows a coppiced area in the second year with abundant *C. palustre* and *Holcus mollis*).

The fruiting heads were counted on forty-two specimens and totalled five thousand three hundred and forty. They ranged in number from 13 to seven hundred and fifty-eight. An exceptionally large specimen produced over 1,200 fruiting heads. The average was $127 \pm 12{\cdot}2$ ($\sigma$ 118; S.E.M. 18·4).

The achenes in ten fruiting heads were 43, 44, 45, 49, 50, 50, 74, 77, 77, an average of $57 \pm 2{\cdot}9$ ($\sigma$ 13·2; S.E.M. 4·4). The average output of achenes from these data would then be $7{,}225 \pm 1{,}015$ per plant.

Canterbury Bell, *Campanula Trachelium*

Like most marginal woodland species the seeds of *Campanula Trachelium* require light for their germination. Kinzel obtained 10 per cent germination, in light only, but Mr. T. A. Dymes informs me that the seeds germinate freely if sown immediately they are ripe, some in the autumn and some the following spring. Although established plants can endure appreciable shade, the species is essentially one of clearings. The number of capsules produced was determined for only twenty-eight plants. They were as follows: 9 capsules (1),

10 (3), 11 (1), 12 (1), 13 (2), 15 (3), 16 (2), 17 (3), 18 (1), 19 (1), 25 (1), 26 (1), 27 (1), 28 (2), 30 (1), 35 (1), 37 (1), 41 (1), 47 (1), an average of $20{\cdot}6 \pm 1{\cdot}2$ capsules per plant ($\sigma$ 10; S.E.M. 1·9). The seeds were counted in nine capsules and numbered 135, 199, 245, 307, 361, 371, 406, 411, 451, an average of $321 \pm 22{\cdot}4$ seeds per capsule ($\sigma$ 101; S.E.M. 33·7). Thus, the average seed output is $6{,}639 \pm 847$ seeds per plant and a reproductive capacity possibly not exceeding 700.

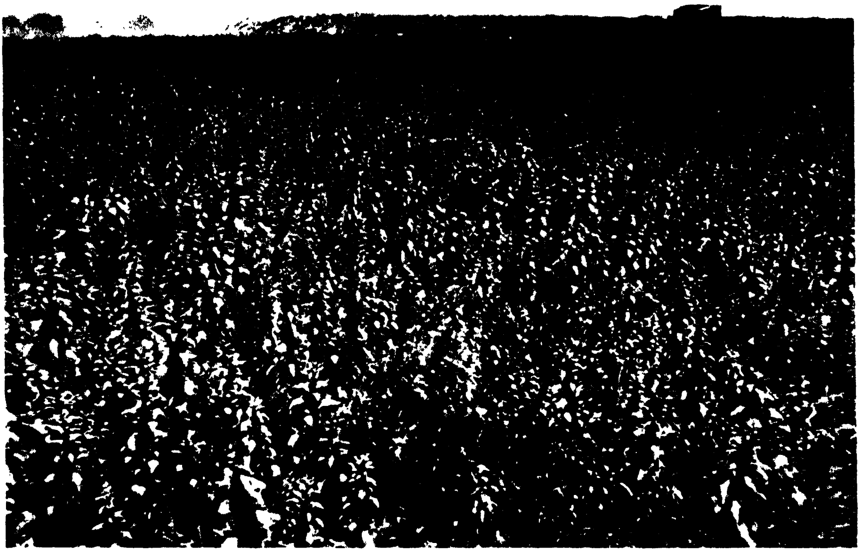
## Species of the Intermittently Open Habitats of Drying, Exposed Mud

Such habitats as these are normally associated with exceptionally dry seasons and their incidence is often very irregular and at long intervals. The characteristic vegetation of these habitats has been briefly described by the writer (1921, *The Naturalist*, pp. 329–33 and 365–66), and the occasional presence on exposed mud of rare species in very large numbers—as, for example, *Rumex limosus*, *Limosella aquatica*, and *Alopecurus fulvus*—to disappear again for perhaps a quarter or half a century, is not merely evidence of the strikingly intermittent character of the conditions requisite for these species but also attests to the prolonged dormancy of their seeds. The latter are often small in size (*cf.* Fig. 31, 1, 4, 6, and 7), though the seeds of *Damasonium* (Fig. 31, 5) are larger. The fruits, too, are often small (Fig. 31, 2 and 3), though here also there are exceptions, such as *Polygonum nodosum* (Fig. 31, 8). That the seeds of such plants do actually remain dormant for long periods in the mud is shown by the fact that viable seeds have been obtained by the writer from the floor of a reservoir at a depth of from six to twelve inches below the surface of the caked mud, and rare species sometimes appear in vast numbers in localities where they have not been seen for many years, and where too a suitable situation for their growth may not have been available for a considerable period.

These characteristics are not confined to flowering plants but have their counterpart amongst the cryptogams. Thus the almost ubiquitous alga, *Botrydium granulosum*, will appear as a vast expanse of green dewdrops on the muddy floor of a reservoir that has not been exposed for half a century, succeeded perhaps by the rosettes of the liverwort, *Riccia crystallina*. The exceedingly rare members of the algal genus *Oedocladium* would appear to be equally characteristic of these intermittently available habitats, and serve to emphasize the reality of the concept that these peculiar habitats have their own peculiar flora.

*Chenopodium rubrum* L.

Although this species is most familiar as a plant of artificial habitats, since such are continuously available (*e.g.* manure heaps), its natural habitat would seem to be the exposed mud of ditches, ponds, reservoirs, and other shallow waters. In dry summers it may appear on the floor of such in remarkable profusion (*cf.* Plate IV, which shows an almost pure stand of this species occupying the floor of a dried-up reservoir). It is the greater familiarity of the artificial habitats which is doubtless responsible for the underestimates



*Chenopodium rubrum* L. occupying the exposed mud of a reservoir in a drought year.

A rare Dock (*Rumex limosus* Thuill.) forming a broad zone round the "Welsh Harp" Reservoir in 1921.

Both marginal and central fruits exhibit two forms, the one with three spines and the other with two. The former type is more or less triangular in cross-section and the latter more flattened. The two-spined type of fruit

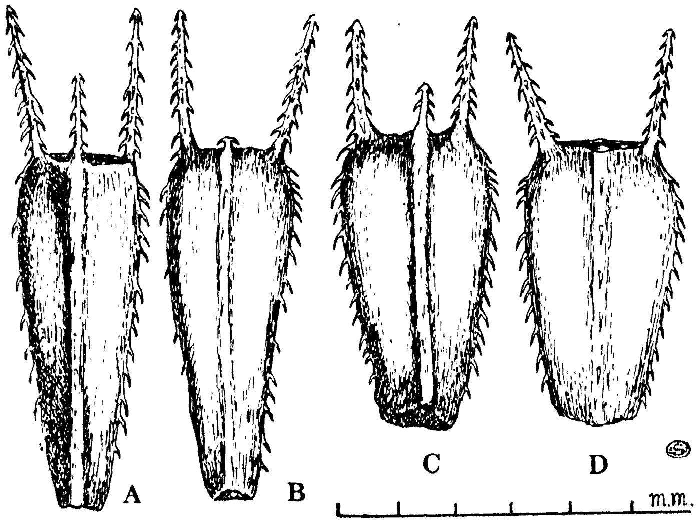


FIG. 30. Fruits of the Burr-marigold (*Bidens tripartita*), showing the four types. A and B, the long, narrow disk fruits. A with three spines and B with two spines and a rudimentary third. C and D, the short and broad marginal fruits, with three and two spines respectively. (All × 7·5.)

not infrequently bears a rudimentary third spine (*cf.* Fig. 30B). The fruits of *Bidens cernua* show a similar difference between the marginal and central fruits, but normally bear three or four spines. The reflexed barbs upon the

TABLE XCV. VARIATION IN NUMBER OF CAPITULA PER PLANT OF *BIDENS TRIPARTITA* L.

| Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals | Number of capitula | Number of individuals |
|---|---|---|---|---|---|---|---|
| 3 | 1 | 19 | 3 | 34 | 1 | 63 | 2 |
| 5 | 4 | 20 | 1 | 35 | 1 | 66 | 1 |
| 6 | 1 | 21 | 4 | 36 | 1 | 72 | 1 |
| 7 | 3 | 22 | 2 | 37 | 1 | 73 | 1 |
| 8 | 5 | 23 | 3 | 39 | 1 | 84 | 1 |
| 9 | 4 | 24 | 3 | 41 | 3 | 96 | 1 |
| 10 | 4 | 25 | 2 | 43 | 1 | 99 | 1 |
| 11 | 4 | 26 | 3 | 44 | 1 | 102 | 1 |
| 12 | 4 | 27 | 1 | 46 | 1 | 111 | 1 |
| 14 | 2 | 28 | 5 | 47 | 2 | 130 | 2 |
| 15 | 1 | 29 | 1 | 50 | 1 | 144 | 1 |
| 16 | 2 | 30 | 1 | 52 | 1 | 161 | 1 |
| 17 | 2 | 31 | 1 | 55 | 1 | | |
| 18 | 1 | 33 | 1 | 61 | 1 | | |

Total of 100 plants, 3,292 capitula.

spines and body of the fruits render the latter readily carried by animals; but they are also dispersed by water, and this is facilitated by their capacity for floating for several days or even weeks. The grapnel-like character of the spines is perhaps most important as an anchoring mechanism.

The smallest of the specimens of *Bidens tripartita* which were examined produced only three capitula and the largest 161 (Table XCV). The latter would, however, be far surpassed by some of the specimens which appear on the floor of large ponds that only infrequently dry up.

The average number of fruiting capitula per plant was $32{\cdot}92 \pm 2{\cdot}12$ ($\sigma$ 31·81; S.E.M. 3·18). The numbers of fruits were counted in twenty-five fruiting heads, and were as follows: 32, 36, 37, 39, 40, 41 (2), 43, 49, 50 (4), 51, 52, 53, 54 (2), 59 (2), 60 (2), 75, 77, 83. Thus the average number of achenes per fruiting capitulum was $50{\cdot}6 \pm 1{\cdot}6$ ($\sigma$ 12·5; S.E.M. 2·5). The average output of fruits per plant was therefore $1{,}669 \pm 160$.

Although no exact data are available for the percentage germination, masses of fruits are often present in drift in which almost everyone has germinated, which indicates that the percentage viability is high.

*Ranunculus sceleratus* L.

This characteristic species of drying mud often attains a very large size on the rich substratum constituting the floor of a pond or reservoir exposed during a period of drought. Under these conditions the normal range of 8–24 inches given by Hooker and Babington is far surpassed, individuals sometimes attaining over 120 cm.

The number of carpels per fruiting head is very large. The achenes were counted on fifty fruiting heads, and totalled 11,393, or an average of 228 ($\sigma$ $227{\cdot}8 \pm 4{\cdot}6$) achenes. Although in view of the wide dispersion a much larger number of specimens would be needed to show a modal value, the

TABLE XCVI. VARIATION IN NUMBER OF CARPELS PER FRUITING HEAD OF *RANUNCULUS SCELERATUS* L.

| Number of achenes | | Number of fruit-heads | Number of achenes | | Number of fruit-heads | Number of achenes | | Number of fruit-heads |
|---|---|---|---|---|---|---|---|---|
| 120 | T | 2 | 208 | | 1 | 259 | | 1 |
| 136 | | 1 | 210 | T | 1 | 261 | T | 1 |
| 156 | T | 1 | 213 | T | 1 | 262 | | 1 |
| 167 | | 1 | 216 | T | 1 | 265 | | 2 |
| 169 | | 1 | 219 | T | 1 | 266 | | 1 |
| 180 | T | 1 | 225 | T | 1 | 268 | | 1 |
| 183 | T | 2 | 230 | | 1 | 270 | T | 1 |
| 185 | | 1 | 231 | T | 3 | 271 | | 1 |
| 186 | T | 1 | 232 | | 1 | 272 | | 2 |
| 189 | T | 1 | 234 | T | 1 | 273 | T | 2 |
| 195 | T | 1 | 237 | T | 1 | 288 | T | 1 |
| 199 | | 3 | 238 | | 1 | 342 | T | 1 |
| 200 | | 1 | 252 | T | 1 | 355 | | 1 |
| 202 | | 1 | 256 | | 1 | | | |

Total of 11,393 achenes in 50 fruit-heads. Average $227{\cdot}8 \pm 4{\cdot}6$; $\sigma$ 48·3; S.E.M. 6·9.

data are of interest as showing an appreciable tendency for the numbers to be some multiple of three. Actually the excess above expectation of the specimens showing hidden trimery is about 18 per cent (*cf.* Salisbury, 1919).

The fruiting heads were counted for only twenty-two specimens. They ranged in number from 11 to three hundred and eighty-one. The average number of achenes was 116±12·9, but it must be emphasized that this is almost certainly a conservative estimate. Even so, these data would indicate an average output of 26,494±2,462 achenes per plant.

Germination, according to E. Lehmann (1911), ranges from 34 to 98 per cent in light, with an average of 62 per cent±5, whilst in darkness it was from 0 to 3 per cent, with an average of 0·6 per cent±0·2. Thus the average reproductive capacity is probably at least 16,400±1,500. The achenes are small, *ca.* 0·9–1·2 mm. in length, and the average weight determined on a sample of 4,000 was only 0·000125 gm. per achene. They are dispersed by water, and from Praeger's observations (R. Lloyd Praeger, 1913) do not float more than 3½ days. Subsequently they sink on to the mud. Here their dormancy, and subsequent germination when the water level falls and the mud is exposed, would, from the researches of Gassner (1915), appear to be determined by the fact that the seeds of this Buttercup do not germinate unless subjected to variations of temperature, and that of the mud is likely to remain relatively constant so long as it is covered by water. Further, although Gassner obtained 28 per cent germination in darkness by the use of fluctuating temperatures, germination in darkness is usually very low, as the data of Lehmann show. When the mud is exposed, however, the dormant achenes resting on the surface are subjected both to a high light intensity and to marked diurnal temperature changes.

Flowering Rush, *Butomus umbellatus* L.

Experience of this species would appear to indicate that the development of seedlings is dependent upon exposed mud and that colonization is intermittent.

Subsequent to establishment the plant extends by means of its rhizomes, and in the northern limit of its geographical range the species is sterile and depends on vegetative spread alone. Such sterility suggests that climatic conditions may account for the appreciably lower figures, for both number of fruits produced by an individual plant and for the number of seeds in the follicles, which Eklund (1929) gives for Finnish specimens as compared with those based upon examination of British plants. The rate of radial spread by growth of the monopodial rhizomes is initially about 8 cm. per annum, and lateral buds from the main axis form branch rhizomes, which, like the main axis, may subsequently produce from one to three inflorescences. As the connections of the laterals with the parent axis persist for some years the number of inflorescences produced tends to increase for a time with the age of the plant. Owing, however, to the competition for food between the component parts of the rhizome system, and because the number of ultimate ramifications tends to augment steadily, the rate of radial extension diminishes, and a diminishing proportion of the crowded branches produce inflorescences.

Quite frequently, indeed, large clumps of this species will produce only a few inflorescences. The actual range observed was from one inflorescence to an exceptionally floriferous plant with seventeen. The total number of follicles per plant born by the specimens examined ranged from 42 to 1,764, and the average for 12 plants was three hundred and ninety-four. Counts of the seeds in individual follicles yielded an average of $88 \pm 3{\cdot}5$. This indicates an average of nearly 35,000 seeds per plant (34,672). Eklund (*loc. cit.*) gives the number of follicles on three plants, viz. 66, 78, and 136, an average of only 93, whilst twelve counts made by him of the number of seeds per follicle shows an average of only 31·1. These figures would indicate an average output of seeds per plant in Finland of about 2,500 per annum, or approximately 1/14 of that for English specimens, a difference which is in conformity with the fact that in the extreme north of its range *Butomus umbellatus* is entirely vegetative (Beyle, M., 1928).

Water-plantain, *Alisma plantago* L.

Although this species is to be found growing in shallow water, and might therefore be supposed to be a plant of relatively permanent habitat conditions, actually colonization by *Alisma plantago* is almost confined to exposed mud subjected to drying. Crocker and Davis (1914, " Delayed germination in Seed of *Alisma plantago* ") showed that drying of the seeds was an important factor for inducing germination, and in its natural habitats the increase in number of individuals is almost invariably the sequel to a prolonged drop in water-level. After the summer droughts of 1919 and 1921 the increase in numbers of individuals of this species in many ponds was spectacular, and with the subsequent rise in water-level some of these individuals persisted where the depth of water remained appreciable. The replacement of such individuals seems to depend mainly, if not entirely, upon the recurrence of another exposure of the mud for a sufficiently prolonged period. We are therefore justified in regarding *Alisma plantago* as belonging to the category of species of intermittent habitats.

The number of carpels in the fruits was determined in 1,200 specimens, and these showed an average of $20 \pm 0{\cdot}08$ carpels per fruit ($\sigma$ 4·4; S.E.M. 0·12).

The total number of fruits counted on a random selection of eleven plants was 20,065, and ranged from 141 to 7,823 fruits per plant. The other nine plants bore respectively 145, 228, 271, 722, 741, 804, 1,600, 2,278, and 5,332 fruits. The average from these data is $1{,}824 \pm 481$ fruits per plant ($\sigma$ 2,385; S.E.M. 722). From these figures the average number of schizachenes produced by a plant each year would be $36{,}518 \pm 9{,}766$, or approximately between 27,000 and 46,000 seeds. Although it is realized that undue stress must not be placed on data from so small a number of specimens, yet it is quite evident that the output of this species is large, as also its reproductive capacity, since the average germination is high and probably about 98 per cent. Each year, so long as the water-level remains high, the fruits, disintegrated into their constituent schizachenes, sink on to the mud and there remain dormant. How many years they can retain their viability is not known, but the carpet

of seedlings of this species which is sometimes to be observed on exposed mud in the summer suggests that the period may be appreciable.

*Alisma ranunculoides* L.

Except for its restriction to more or less peaty localities this species occupies similar situations to *Alisma plantago*. Depauperate forms are to be met with in dune slacks, and in these the species is regularly to be found on some dune systems, as from their nature dune slacks almost regularly dry up, either wholly or in part, every summer. Here, then, it is perhaps scarcely appropriate to regard the species as occupying a truly intermittent habitat, and it may well be that the lower output that these slack plants produce as compared with the normal form is not detrimental to the persistence of the species, owing to the regularity with which a suitable habitat is provided.

For the depauperate dune forms at Southport the arithmetic mean for the number of carpels per flower in 200 flowers was found to be $22 \pm 0{\cdot}26$, with a standard deviation of 5·5 and a standard error of the mean of 0·39. For the normal type the average was $32 \pm 0{\cdot}2$, with a standard deviation of 4·4 and a standard error of 0·31 (*cf.* Salisbury, E. J., 1926, " Floral Construction in the Helobiales "). Of these carpels, however, some usually abort, the proportion being 5·5 per cent, so that we can assume the normal production of achenes per flower to be $30{\cdot}24 \pm 0{\cdot}2$.

The number of mature fruiting heads produced by individual plants was determined for sixty specimens, as follows: 4, 5, 6, 7 (2), 8, 9, 10, 11, 12 (2), 13, 14 (3), 15 (4), 16 (3), 17, 18, 19 (3), 20, 21 (2), 23 (2), 24, 26, 27 (2), 29, 30 (2), 32 (2), 34 (1), 35, 37 (2), 38, 40, 41 (2), 42, 43, 45, 47, 50, 51, 52, 72, 78, 86. The average is $26{\cdot}7 \pm 1{\cdot}4$ ($\sigma$ 17·2; S.E.M. 2·2). The average output of achenes per plant is thus $807 \pm 43$.

Like *Alisma plantago*, this species increases after periods of drought, and from the very striking fluctuations in population which the writer has observed in some of its localities it would appear probable that it is a short-lived perennial. *A. ranunculoides* can increase vegetatively by means of offsets, which are stolon-like in the *var. repens*, but normally such vegetative increase appears to be insignificant.

When submerged cleistogamous flowers can be formed.

Starfruit, *Damasonium stellatum* Pers. (*D. Alisma* Mill.)

This interesting and now very rare species appears to have decreased in most of its stations and to have become extinct in many (*cf.* Salisbury, E. J., 1927, " The Waning Flora of England "). It has become extinct in five of the counties where it formerly occurred and has diminished markedly in at least four others. In Hertfordshire the diminution appears to have been progressive over a long period (*cf.* Salisbury, E. J., 1924 (b), " Changes in the Hertfordshire Flora "); but it is worthy of note that there was a marked increase of the population of this species in certain localities in the dry summer of 1938. In one pond where there had been no individuals the previous year a considerable number appeared some weeks after all free water had

evaporated upon the exposed mud in the central area as well as towards the margins (*cf.* Plate V).

It is quite evident that *Damasonium stellatum* is very dependent upon exposed mud for its establishment, and though it may, and indeed does, persist in small numbers in some stations where there is a shallow shelving margin, its pronounced diminution in our flora may well be due not only to the general lowering of the water table (Salisbury, 1927), with consequent decrease in the number of potential habitats, but also to the fact that with the increased attention to ponds, etc., as compared with bygone times, their margins tend to be maintained in a less shelving condition, so that it is only in years of extreme drought that any appreciable augmentation of the population can occur.

In over two thousand fruit-heads examined six carpels were always present, and in a considerable number of those which were dissected there were two seeds in each carpel. Although it is extremely probable that one of the seeds occasionally aborts, and that less than six carpels may be produced, it may be assumed for the purposes of estimation that each fruit produces twelve seeds.

TABLE XCVII. VARIATION IN NUMBER OF FRUITS PER PLANT OF *DAMASONIUM STELLATUM* PERS.

| Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals | Number of fruits | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 1 | 12 | 1 | 25 | 1 | 53 | 1 |
| 2 | 3 | 13 | 8 | 26 | 1 | 58 | 1 |
| 3 | 3 | 14 | 5 | 27 | 3 | 60 | 1 |
| 4 | 3 | 15 | 3 | 29 | 1 | 63 | 2 |
| 5 | 4 | 16 | 4 | 30 | 2 | 64 | 1 |
| 6 | 5 | 17 | 4 | 32 | 1 | 73 | 1 |
| 7 | 5 | 18 | 5 | 33 | 1 | 108 | 1 |
| 8 | 6 | 19 | 5 | 35 | 2 | 126 | 1 |
| 9 | 7 | 20 | 1 | 39 | 1 | | |
| 10 | 8 | 21 | 1 | 43 | 1 | | |
| 11 | 4 | 22 | 2 | 50 | 1 | | |

Total for 111 plants 2,137 fruits.

The average number of fruits per plant was thus $19{\cdot}25 \pm 1{\cdot}25$ ($\sigma$ 19·8; S.E.M. 1·88), or $231 \pm 15$ seeds per plant. Judging by the few tests that have been made the germination would appear to be low, possibly not over 25 per cent. This would indicate a reproductive capacity of about 58 potential offspring per plant.

*D. stellatum* is stated to be perennial. Personally I have not succeeded in maintaining a plant alive after flowering and fruiting, although a number were raised from seed and appeared perfectly healthy. A considerable number of plants in their natural habitat likewise died after fruiting, so the species is perhaps either monocarpic or a short-lived perennial. In view of the very small seed output and low reproductive capacity the rarity of the species is not surprising, especially if the individuals only fruit once.

In view of the fact that *Alisma plantago*, *Alisma ranunculoides* and *D. stellatum* all occupy similar habitats and all normally require exposed mud for the free germination of their seeds, it is of considerable interest to note how their respective seed outputs, and probably their reproductive capacities also (though germination data for *A. ranunculoides* is lacking), are in conformity with their relative frequencies and abundance. *A. plantago* occurs in all the counties and vice-counties of Ireland, and in 101 of the 112 of Great Britain. In most of these areas, except the extreme north, the species is common. *A. ranunculoides* occurs throughout Ireland also, and in 91 comital and vice-comital areas of Great Britain. Not only is its area thus more restricted but it is less abundant in Ireland than its congener and far less so in Great Britain. *D. stellatum* is absent from Ireland and Scotland, and has only been recorded from fifteen counties in England. From five of these it has now apparently disappeared and is very rare in the remainder. The average seed outputs, as we have seen, approximate to: 36,000 per plant for *A. plantago*; 1,060 per plant for *A. ranunculoides*; 230 per plant for *D. stellatum*, a gradation that is accentuated by the high germination of the first-named and the low germination of the last. The mode of seed dispersal is probably the same for all three species, namely by water and occasionally in mud on the feet of birds, and there is no reason to suppose there is any difference in the efficiency of dispersal between the three species. The seed, which is *ca.* 2·5 mm. in length, is shown in Fig. 31, 5.

Redshank, *Polygonum nodosum* Pers. (*P. maculatum* Trimen and Dyer)

This is one of the more characteristic species of drying mud. Unfortunately only a few fruit counts of this species have been made, and none from the very large specimens which are found on the floor of dried-up ponds and reservoirs. Five small plants bore 170, 455, 553, 587, and 1,074 fruits respectively, whilst a medium-sized plant produced 9,200 fruits. The large specimens, it is estimated, may have produced some 25,000 fruits. The output of this species has an average value that is at least 2,000 fruits per plant, and probably much larger (Fig. 31, 8).

*Rumex maritimus* L. and *Rumex limosus* Thuill (*R. palustris* Sm.)

Both these Docks are very local and generally regarded as rare, but when a mere or reservoir dries up they may suddenly appear in very large numbers from dormant seeds in the mud (*cf.* Salisbury, E. J., *Yorkshire Naturalist*, *loc. cit.*). Thus, in the very dry summer of 1921, *R. limosus* appeared in vast numbers on the exposed mud of the " Welsh Harp " at Hendon (*cf.* Plate IV), whilst in the dry summers of 1934 and 1935 both this species and *R. maritimus* were conspicuously abundant in the exposed floors of the Breckland meres. Germination experiments with sun-baked seeds of *R. maritimus* yielded 98 per cent germination, and similarly high values have been obtained with seed of *R. limosus*. Exact data for the seed output of these species are not available, but careful estimates for five plants of *R. limosus* indicated seed outputs of approximately 24,000, 43,000, 66,000, 67,000, and one hundred and eighteen thousand. The average of these is therefore about 64,000 seeds per

PLATE V

The Star-fruit (*Damasonium stellatum* Pers.) a rare plant growing on the cracked mud occupying the floor of a pond that had not been dry for many years previously. (The stick is two inches long.)

*Limosella aquatica* L. showing vegetative spread by runners. This was part of a zone of this rare species extending round a reservoir after the water had receded in a very dry summer.

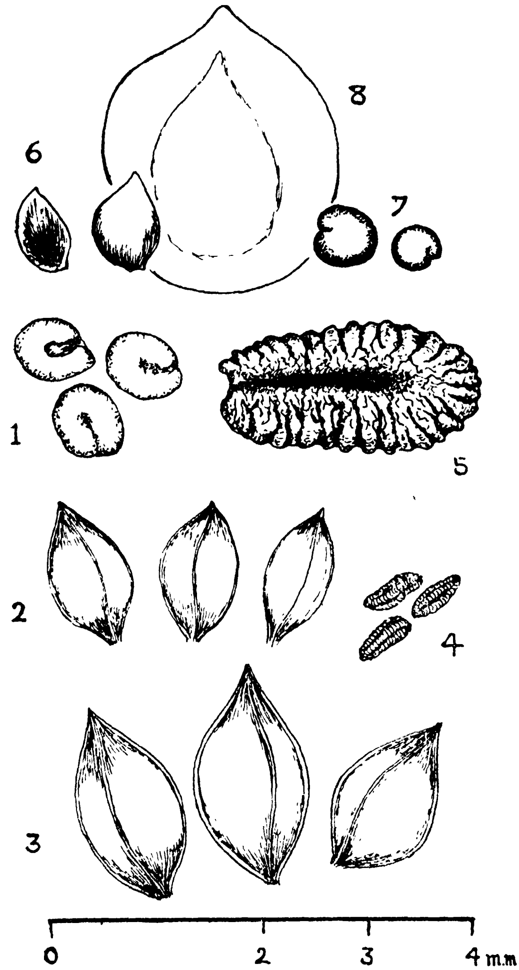



FIG. 31. SEEDS AND FRUITS OF SPECIES OF EXPOSED MUD. Fig. 1. Seeds of the Marsh Cress (*Nasturtium palustre*). Fig. 2. Fruits of the Golden Dock (*Rumex maritimus*). Fig. 3. Fruits of the Marsh Dock (*Rumex limosus*). Fig. 4. Seeds of the Mudwort (*Limosella aquatica*). Fig. 5. Seed of the Starfruit (*Damasonium stellatum*). Fig. 6. Seeds of the Lesser Loostrife (*Lythrum hyssopifolium*). Fig. 7. Seeds of the Red Goosefoot (*Chenopodium rubrum*). Fig. 8. Fruit of the Redshank (*Polygonum nodosum*). All figures to the same scale (× 14).

plant. The very large specimens that often occur on the freshly exposed mud may produce well over 200,000 seeds. The output of *R. maritimus* is appreciably lower but still large (Fig. 31, 2 and 3).

*Limosella aquatica* L.

This rare species of drying mud is also liable to appear suddenly in large numbers. Unlike the previous species considered the individual plants are of small size but spread very rapidly by means of their runners. Through the efficiency of its vegetative propagation, however, the seed production is by no means inconsiderable.

A well-grown plant was found to bear 72 fruits and fifteen runners, each of which would in turn produce a rosette and subsequently more fruits. The capsules on sixty-three plants totalled 1,963, an average of $31{\cdot}1 \pm 1{\cdot}6$ fruits per plant ($\sigma$ 19·3; S.E.M. 2·4). The smallest plant had three capsules and the largest seventy-five. It should, however, be mentioned that under favourable conditions the average may be much nearer the latter figure. The seeds (Fig. 30) were counted in twenty-one capsules, and ranged from 64 to 184 (64, 93, 104, 112, 116, 123, 124, 132, 136, 139, 141, 142, 146 (2), 148, 154 (2), 155, 168, 175, 184) an average of $136 \pm 4$ seeds per capsule ($\sigma$ 27·2; S.E.M. 6). The average seed output, therefore, is $4{,}236 \pm 324$ seeds per plant, a very high figure, having regard to the small size of the plant and the efficient means of vegetative propagation. In a crowded community of rather small plants the yield per unit area is probably as high as where the individuals are more scattered and larger (Fig. 31, 4).

*Juncus bufonius* L.

The size of plants of this species is extremely variable, as it is another example of a species which commonly occurs either sparsely, when the individuals are comparatively large, or as numerous small and crowded plants. The yield per unit area of the mud is very similar in the two conditions. According to Stevens (*loc. cit.*) an average-sized specimen of this species produces 5,300 seeds. But my own data from plants in damp coppiced woods and exposed mud of ponds indicates an average of about 34,000 seeds per plant when growing in the non-crowded condition, and large specimens will yield over 50,000 seeds. The smaller crowded specimens make up in their numbers what they lack in size. The average number of seeds per capsule was 105.

Marsh-cress, *Nasturtium palustre*

Although the data for this species are scanty it is so characteristic of drying mud, where it sometimes occurs in extraordinary profusion, that an indication of its output is desirable. A specimen from the Welsh Harp which was below the average size had 307 ripe fruits, and another smaller specimen bore one hundred and thirty-one. Eklund gives data for two plants with 195 and 206 fruits respectively. These figures indicate an average of about 200 fruits per plant, whilst each pod produces an average of about 65 seeds. Thus the

average output per plant would be about 13,000 seeds. Mitchell's experiments (1926, *loc. cit.*) gave a germination of only 30 per cent in light, and no germination in the dark. This suggests a reproductive capacity of perhaps not more than about 4,000 per plant. It should, however, be mentioned that on freshly exposed mud this species often attains a very large size, with correspondingly augmented output (Fig. 31, 1).

Brookweed, *Samolus valerandi* L.

Data for the fruit production of the Brookweed have only been obtained during an unfavourable season, when the general growth was below the average. The number of fruits ranged from 5 to 234, and in fifty-five individuals was as follows: 5 (2), 6 (3), 7 (4), 8 (1), 9 (2), 10 (1), 11 (4), 16 (2), 18 (1), 19 (2), 20 (1), 21 (1), 22 (1), 23 (1), 25 (2), 27 (1), 29 (1), 33 (1), 34 (2), 35 (1), 37 (1), 39 (1), 41 (1), 42 (1), 44 (1), 46 (1), 53 (1), 59 (1), 60 (1), 66 (1), 68 (1), 86 (1), 98 (1), 101 (1), 106 (1), 128 (1), 135 (1), 182 (1), 209 (1), 234 (1), an average of $44{\cdot}3 \pm 4{\cdot}5$ fruits per plant ($\sigma$ 50·0; S.E.M. 6·7). The seeds were counted in twenty-two capsules, including a random sampling of three from depauperate individuals (17–42 seeds) and three from very vigorous individuals (70–122 seeds). The numbers of seeds were as follows: 17, 20, 29, 41, 42, 42, 45, 54, 56, 64, 68, 70, 72, 76, 77, 82, 85, 103, 104, 108, 114, 122. The average was $68 \pm 4{\cdot}2$ ($\sigma$ 29·5; S.E.M. 6·27). The average output of these specimens would thus be $3{,}031 \pm 492$ seeds per plant. Only one germination test was carried out, and this gave an average germination of 64 per cent, which would give an average reproductive capacity of 1,939 potential offspring per plant. The small angled seeds are shown in Fig. 1, 12.

It is certainly true that some of these species of intermittently available habitats are large-sized plants, so that it is of interest to know whether species whose individuals are normally small and which frequent such habitats are also characterized by relatively large seed outputs. Curiously the vegetation of drying mud not only includes some of our largest monocarpic species but also our smallest phanerogams. Three very characteristic plants of intermittent habitats are *Sedum villosum*, *Radiola linoides*, and *Centunculus minimus*. The last is the smallest British flowering plant, whilst the other two are amongst our smallest annuals, comparable with *Erophila* in the dune flora.

*Sedum villosum* L.

Thirty-seven fruiting specimens of this species were examined. All the fruits consisted of five carpels, and the number of carpels per plant was as shown in Table XCVIII.

The average number of carpels per plant was $44 \pm 2{\cdot}1$ ($\sigma$ 19·4; S.E.M. 3·2). The number of apparently fertile seeds per carpel ranged from six to fourteen, as follows: 6 (1), 7 (4), 8 (2), 9 (4), 13 (1), 14 (1), an average of $8{\cdot}7 \pm 0{\cdot}39$ seeds per carpel ($\sigma$ 2·11; S.E.M. 0·58). Thus the average number of seeds per plant was $383 \pm 35$.

TABLE XCVIII. VARIATION IN NUMBER OF CARPELS PER PLANT OF *SEDUM VILLOSUM* L.

| Number of carpels | Number of individuals | Number of carpels | Number of individuals |
|---|---|---|---|
| 15 | 2 | 50 | 6 |
| 20 | 3 | 55 | 6 |
| 25 | 2 | 65 | 1 |
| 30 | 4 | 70 | 1 |
| 35 | 2 | 85 | 1 |
| 40 | 5 | 115 | 1 |
| 45 | 3 | | |

Average 44 carpels per plant.

*Lythrum hyssopifolium* L.

Only sixteen plants of this rare species were examined. The number of capsules ranged from 27 to 187, with an average of 73·3±10·5. The average number of seeds per capsule was 25±1. These data would indicate a seed output of 1,843±336 seeds per plant. The specimens studied were small, compared, for instance, with those characteristic of the exposed mud of ditches in Brittany. The seeds (Fig. 31, 6) are about 0·8–0·9 mm. long by about 0·5–0·6 broad and concavo-convex.

Mousetail, *Myosurus minimus* L.

Although the most vigorous infructescences of this species may attain a height of six inches the vegetative organs are small and the total photosynthetic surface very restricted. It is usually found in damp parts of cornfields, cart ruts, and similar places that are more or less inundated in winter, but, as C. E. Salmon states in " The Flora of Surrey," is quite uncertain in its appearance from year to year. One hundred plants bore from 1 to 31 fruit-heads: 1 (12), 2 (10), 3 (20), 4 (13), 5 (9), 6 (10), 7 (12), 8 (5), 9 (1), 10 (2), 11 (2), 12 (2), 13 (1), 31 (1), an average of 4·9±0·25 ($\sigma$ 3·8; S.E.M. 0·38). Each elongating receptacle bears from ninety to three hundred and forty-five achenes, with an average of about 222±21 ($\sigma$=90). The average number of achenes per plant is therefore probably about 1,100±160, a remarkably high number having regard to the small area of leaf surface.

*Tillaea muscosa* L.

This minute Crassulaceous plant of damp sandy places, although often encountered in successive years in the same locality, exhibits very striking fluctuations of population. In very dry years there may be no individuals, or only a few, and these perhaps less than a square centimetre in area, whereas in favourable seasons the individuals may not only be locally abundant but attain to over 25 sq. cm. The fruits were counted on ninety-two plants from various localities and in several seasons. They ranged in number from four fruits to four hundred and fifty-six. The average number of fruits per plant was 92±5·06 ($\sigma$ 74·4; S.E.M. 7·6). Each fruit consists of from three to five follicles, and the follicles normally contain two seeds each (Fig. 1, 6, p. 6), the average number of seeds per fruit being eight. Thus the average output would be 736±40 seeds per plant. Sixty-three per cent of the plants examined produced less than the mean number of fruits. It is, however, evident that

here, as also with regard to *Radiola linoides*, the output is very high, having regard to the small area of photosynthetic surface which the plant develops.

Allseed, *Radiola linoides* Roth.

This species, though far more frequent and abundant than *Centunculus minimus*, occupies similar habitats. It exhibits striking fluctuations in both abundance and size, and though less intermittent in its appearance than *Centunculus minimus* its occurrence, even in localities where it is regularly present, is usually of a migratory character, and hence may be regarded as a species of intermittent habitats. Individuals exhibit a wide range of size. Eighty-four specimens produced from 4 to 796 fruits, with an average of $96 \pm 8{\cdot}7$ ($\sigma$ 120; S.E.M. 13·1). All the fruits examined contained eight seeds, so that the average seed output would be $768 \pm 69{\cdot}6$. This average is perhaps misleading, as *Radiola* tends to grow as a social species to a greater degree than either *Myosurus*, *Tillaea*, or even *Centunculus*, so that on the basis of yield per unit area the output of *Radiola* might considerably exceed that of the other species.

Chaffweed, *Centunculus minimus*

This rare and extremely small plant, often under two centimetres high, is in some seasons represented by but a few individuals and in others by large numbers, so that the output per unit area is very considerable. In Table XCIX the fruit production of 229 specimens is presented and shows an average of $14{\cdot}18 \pm 0{\cdot}7$ capsules per plant ($\sigma$ 16·9; S.E.M. 1·1). The seeds were counted in twenty capsules; their number varied as follows: 7 (1), 9 (2),

TABLE XCIX. VARIATION IN NUMBER OF CAPSULES PER PLANT OF *CENTUNCULUS MINIMUS* L.

| Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals | Number of capsules | Number of individuals |
|---|---|---|---|---|---|---|---|
| 1 | 4 | 13 | 9 | 26 | 2 | 49 | 1 |
| 2 | 6 | 14 | 4 | 28 | 1 | 56 | 1 |
| 3 | 9 | 15 | 6 | 29 | 3 | 57 | 1 |
| 4 | 14 | 16 | 8 | 30 | 1 | 59 | 1 |
| 5 | 16 | 17 | 7 | 34 | 1 | 60 | 1 |
| 6 | 20 | 18 | 7 | 39 | 1 | 69 | 1 |
| 7 | 15 | 19 | 6 | 40 | 2 | 89 | 1 |
| 8 | 16 | 20 | 3 | 41 | 1 | 93 | 1 |
| 9 | 18 | 21 | 5 | 42 | 1 | 99 | 1 |
| 10 | 8 | 22 | 2 | 43 | 1 | 143 | 1 |
| 11 | 6 | 24 | 2 | 44 | 1 | | |
| 12 | 11 | 25 | 1 | 46 | 1 | | |

Total of 3,249 fruits on 229 plants.

12 (3), 13 (1), 15 (1), 16 (1), 17 (1), 20 (3), 21 (3), 22 (1), 23 (1), 26 (1), 30 (1), a total of 346 seeds, or an average of $17{\cdot}3 \pm 2{\cdot}9$ ($\sigma$ 5·95; S.E.M. 4·4). The average production of seeds per plant was therefore $245 \pm 23$, which is appreciably higher than the average for *Erophila praecox*, although possessing a much smaller photosynthetic surface.

It is worth while calling attention to the fact that both the Gentianaceous and Orchidaceous plants which are characterized by high seed outputs in relation to their size contain representatives which are often remarkably intermittent in their occurrence, a feature that may be associated with an intermittence in the requisite habitat conditions. M. Pilaud (1929, *Bull. Soc. Bot. Fr.* p. 541), has described how large colonies of *Chlora perfoliata* disappear and are not replaced by their offspring, a feature to be observed here as well as in France, and shared by *Cicendia filiformis*; but the environment favoured by the latter is obviously of an intermittent character. Amongst the Orchids the most striking example is perhaps *Orchis morio*, which will appear in vast numbers and disappear as suddenly and completely. So too *Ophrys apifera* will appear in abundance and then die out completely after flowering. I know one such area in which *O. apifera* was exceptionally abundant, over ten years ago, and in which, despite careful search, no specimen has been seen since, although visually the environment would seem unchanged.

## Shingle-Beach Species

Two species of the shingle-beach are strikingly intermittent in their occurrence, namely *Rumex crispus var. trigranulatus* and *Glaucium luteum*, both of which often occur in large numbers over stretches of shingle, and then, after flowering, may become scarce or even disappear. This may be due to the infrequent occurrence of conditions favourable for dispersal of the seeds and colonization, both of which are mainly dependent on the coincidence of a high tide with an appropriate storm at the right season. But whatever the causes the fact is indisputable that these species alike occur intermittently.

*Glaucium luteum* Scop.

The data for this species have been dealt with in another connection. As we have seen, the seed output is $4{,}800 \pm 389$ seeds per plant. Sometimes it is a short-lived perennial, but most commonly is monocarpic and either annual or biennial.

*Rumex crispus var. trigranulatus* Syme.

Although exact counts of the fruits produced were not made, their numbers were fairly closely estimated for a number of individuals, and these estimates indicated that the fruit production normally ranged from about 25,000 to 40,000 per plant, so that the average may be taken as about thirty thousand.

Germination tests carried out by Miss Adams yielded from 97 to 98 per cent, so that the average reproductive capacity would be about 29,000 offspring per plant.

*Beta* (*vulgaris*) *maritima* L.

Unlike the preceding species the Wild Beet is a long-lived perennial, but the natural habitats it occupies are only intermittently available for colonization and/or seed dispersal.

A very small specimen produced not more than 180 " fruits," each with two to three seeds. A large, well-grown specimen was estimated to have

produced some 130,000 fruits, or over 300,000 seeds. We shall probably not be far wrong in assessing the average output of an adult plant as at least 100,000 seeds.

*Limonium binervosum* C. E. Salmon (*Statice binervosum* G. E. Sm.)

This species of Sea Lavender occupies two rather different types of habitat, on shingle as well as situations on rocks. Sometimes *L. binervosum* occurs where there is more or less stable shingle, with the interstices occupied by sandy mud, such as is to be found in " shingle lows " and on the flanks of stabilized " shingle hooks." Such situations, though of a much more permanently open character than the other type of shingle habitat, produce plants which, though numerous, are often of small size, and, at Blakeney Point, yield an average of about 472 fruits per plant. On fine shingle, or such resting on sandy mud, resulting from the intermittent action of storms, *L. binervosum* attains its greatest size and productivity. The average number of fruits per plant at Blakeney Point produced by individuals from these situations was 2,234, or over four times that of plants in the more stable and continuous habitat. In the permanently open habitats of rock faces *L. binervosum* may attain as large a size as in fine shingle resting on sandy mud. It is thus evident that this species is neither definitely in the category of plants of intermittently available habitats nor of permanently open ones, although the bias is towards the former, where its greatest productivity is more commonly developed.

*Limonium rariflora* O. Kuntz (*Statice rariflora* Drej. *L. humile* Mill.)

This species of the same genus has an intermediate status for slightly different reasons. It is a colonizer of the early phases of the salt-marsh, and tends to disappear and become replaced by the far commoner *S. limonium* as the vegetation becomes closed. Since the succession on a salt-marsh is a comparatively rapid one the availability of habitats for this species is of an intermittent character, but their suitability for colonization is of longer duration than the intermittently open habitats already considered. Moreover, the phase at which *L. rariflora* arrives is one in which the vegetation of the salt-marsh is already in a semi-closed condition.

The seed production was determined for twenty-two plants, as follows: 96, 99, 100, 102, 120, 131, 132, 164, 168, 190, 191, 192, 194, 196, 205, 206, 212, 218, 238, 299, 473, 534, a total of 4,460, or an average of $203 \pm 1{\cdot}2$ per plant ($\sigma$ 84·4; S.E.M. 1·8). This is a low average output, having regard to the somewhat intermittent character of the habitat, and more what might have been expected of a species in a community of more secular succession. Hence it is scarcely surprising that *L. rariflora* is a rare species. It occurs in 33 per cent of the counties and vice-comities of Great Britain (England 55 per cent, Scotland 9·7 per cent), but is local, and, as already indicated, disappears from a locality as the succession advances.

From the data in Table C the mean productivity for the thirty-eight species characteristic of habitats that are only intermittently available for colonization is seen to be approximately 28,200 seeds per plant, as compared with an average productivity of just over 3,000 seeds per plant for thirty-eight

TABLE C. SUMMARY OR DATA FOR SPECIES OF INTERMITTENTLY AVAILABLE HABITATS

(*A*) *Species of Coppiced Areas and Clearings in Woods*

| Species | Average output per plant | Average reproductive capacity | |
|---|---|---|---|
| Luzula multiflora | 1,245±208 | | |
| Galeopsis tetrahit | *ca.* 2,010±384 | 720 ? | |
| Epilobium montanum | 2,480±207 | 2,331 | |
| Dipsacus sylvestris | 2,960±405 | | |
| Solidago virgaurea | ? *ca.* 4,000 | | |
| Lychnis dioica | 7,193±1,124 | | |
| Cirsium palustre | 7,225±1,015 | | |
| Epilobium tetragonum | 7,230±673 | 6,435 | |
| Gnaphalium sylvaticum | 9,042±991 | | Mean output for eighteen species of woodland clearings 34,510 seeds per plant. |
| Senecio sylvaticus | 10,638±954 | | |
| Dipsacus pilosus | 11,749±3,370 | | |
| Inula Conyza | 47,000 | | |
| Scrophularia nodosa | 48,090±5,571 | 27,900 | |
| Atropa Belladonna | 74,000 | | |
| Epilobium angustifolium | >76,000 | | |
| Digitalis purpurea | 85,551±7,104 | 81,000 | |
| Verbascum Lychnitis | 88,211±5,968 | | |
| Verbascum Thapsus | 136,500±31,800 | 108,800 | |

(*B*) *Species of Exposed Mud*

| | | | |
|---|---|---|---|
| Centunculus minimus | 245±23 | | |
| Damasonium stellatum | 231±15 | 58 ? | |
| Sedum villosum | 383±35 | | |
| Tillaea muscosa | 736±40 | | |
| Radiola linoides | 768±69·6 | | |
| Alisma Ranunculoides | 807±43 | | |
| Myosurus minimus | 1,100±160 | | |
| Lythrum hyssopifolium | ? 1,843±336 | | |
| Bidens tripartita | 1,669±160 | | Mean of twenty mud species 20,194 seeds per plant. |
| Bidens cernua | 1,847±216 | | |
| Polygonum nodosum | over 2,000 | | |
| Samolus valerandi | 3,031±492 | 1,939 ? | |
| Limosella aquatica | 4,236±324 | | |
| Nasturtium palustre | *ca.* 13,000 | | |
| Ranunculus sceleratus | 26,494±2,462 | *ca.* 17,000 | |
| Juncus bufonius | *ca.* 34,000 | | |
| Butomus umbellatus | *ca.* 35,000 | | |
| Alisma plantago | 36,518±9,766 | 3,580 | |
| Rumex limosus | *ca.* 64,000 | | |
| Chenopodium rubrum | ? *ca.* 176,000 | | |

(*C*) *Species of Shingle*

| | | |
|---|---|---|
| Glaucium luteum | 4,800±389 | |
| Rumex crispus v. trigranulatus | ? 30,000 | |
| Beta maritima | ? 100,000 | |

Mean of forty-one species of intermittent habitats 28,289 seeds per plant.

species of permanently open habitats. The average for twenty-two species of semi-open habitats was approximately 2,500 seeds; for species of closed but unshaded habitats the average was 1,645, whilst for the shade species of woodlands the average was 280 seeds per plant.

### Summary of Seed Production in relation to Habitat

The data that have been furnished in this section present a very wide range of seed output. On the basis of the averages, the species of intermittently available habitats have by far the largest output, followed in diminishing order by the species of permanently open habitats, those of semi-open habitats, those of closed but unshaded habitats, and, lowest of all, those of shaded habitats. But here, as in treating of the seed weights in an earlier chapter, the averages are apt to be unduly affected by a few high outputs, and in the accompanying table the outputs have been classified into thirteen classes, the magnitude of the upper limit of each being twice that of the preceding class.

| | | Habitats | | | | |
|---|---|---|---|---|---|---|
| Output | Class | Permanent open | Semi-open | Closed | Shaded | Inter-mittent |
| 0–50 | I | 1 ( 2·4%) | 1 ( 4·5%) | 0 | 7 (31·8%) | 0 |
| 50–100 | II | 1 ( 2·4%) | 1 ( 4·5%) | 1 ( 4·5%) | 4 (18·1%) | 0 |
| 100–200 | III | 3 ( 7·3%) | 1 ( 4·5%) | 1 ( 4·5%) | 3 (13·6%) | 0 |
| 200–400 | IV | 5 (12·2%) | 5 (22·7%) | 3 (13·6%) | 4 (18·1%) | 3 ( 7·3%) |
| 400–800 | V | 6 (14·6%) | 3 (13·6%) | 3 ( 9·0%) | 2 ( 9·0%) | 2 ( 4·9%) |
| 800–1,600 | VI | 8 (19·5%) | 3 (13·6%) | 4 (18·0%) | 1 ( 4·5%) | 5 (12·1%) |
| 1,600–3,200 | VII | 6 (14·6%) | 2 ( 9·1%) | 6 (27·0%) | 1 ( 4·5%) | 7 (17·0%) |
| 3,200–6,400 | VIII | 8 (19·5%) | 2 ( 9·1%) | 4 (18·0%) | 0 | 2 ( 4·9%) |
| 6,400–12,800 | IX | 0 | 4 (18·2%) | 1 ( 4·5%) | 0 | 6 (14·6%) |
| 12,800–25,600 | X | 3 ( 7·3%) | 0 | 0 | 0 | 1 ( 2·9%) |
| 25,600–51,200 | XI | 0 | 0 | 0 | 0 | 7 (17·0%) |
| 51,300–102,400 | XII | 0 | 0 | 0 | 0 | 6 (14·6%) |
| 102,400–204,800 | XIII | 0 | 0 | 0 | 0 | 2 ( 4·9%) |
| Total species | | 41 | 22 | 23 | 22 | 41 |
| Average scale value | | 6·0 | 5·68 | 6·0 | 2·85 | 8·7 |
| Standard error of mean | | 0·331 | 0·502 | 0·377 | 0·386 | 0·42 |
| Variance | | 4·39 | 5·308 | 3·18 | 2·827 | 7·07 |

It is evident that there is little significant difference between the species of the unshaded closed communities and the species of semi-closed habitats, but that the output of the species of shady habitats tends to be much lower, with a mean class value of only 2·85, and fifty per cent of the species in classes I and II. On the other hand the species of habitats which are intermittently available have a mean class value of 8·7, and over 43 per cent of the species are in classes VI, VII, and IX, whilst thirty-six per cent of the species are in classes XI to XIII that are unrepresented in the other habitat categories.

The contrast between the species of permanently and intermittently available habitats is striking and significant (Difference of means 2·7; S.E.D. 0·532).

Thus the species of intermittent habitats have far the largest seed outputs, a feature the more significant in that the weight of the seeds of the species of open habitats are in general lighter.

It should be noted that even so low a seed output as that of *Damasonium stellatum* ($231 \pm 15$) enables the species to survive, and indeed there are no

grounds to warrant belief that its diminution and local extinction are in any way connected with a high mortality but rather that its low reproductive capacity prevents its effective exploitation of suitable habitats on the increasingly infrequent occasions when these become available under modern conditions.

The species of intermittent habitats would appear either to have acquired the capacity to produce such large numbers of seeds or they have occupied such habitats because they already possessed that quality, not because their mortality rate is, in general, any higher than that of other species but because their frequency and abundance are alike dependent upon rapid exploitation of a transient phase of the environment they occupy.

The lowest output probably provides a quite adequate margin of safety against the normal risks of mortality; but though a low output does not necessarily lead to any diminution it does tend to impose rarity. Indeed, the risks of mortality are probably greatest for those species which are most abundant, because predators and parasites alike are liable to rapid increase and spread. The vast assemblages of the species of intermittent habitats which are sometimes seen, however, probably escape because of their short tenure, which does not permit the building up of a corresponding host of their enemies.

### Seed Production and Mutation Rate

There is the possibility that the seed production of species might be negatively correlated with the rate of mutation, a low mutation rate being perhaps compensated by a large seed output.

Unfortunately the data as to mutation rates of different species at present available are extremely meagre. It would appear that the mutation rate of the Sweet Pea is a low one, and probably very much lower than that of *Primula sinensis* (*cf.* Crane and Lawrence, 1938, " The Genetics of Garden Plants," pp. 44 and 54), which has a much larger seed output; but the comparison is here confused by the vastly different weights of the seeds of the two species.

The mutation rate of *Antirrhinum*, which has seeds more comparable in size to those of *Primula*, is normally high, despite the fact that the reproductive capacity of the Snapdragon is large. Where there is biological isolation, as in apomictic genera such as *Taraxacum* and *Antennaria*, or such normally self-fertilized genera as *Erophila* and *Capsella*, the absence of any masking of mutations by interbreeding renders it likely that we can utilize the numbers of microspecies as an indication of the frequency of mutations. On this basis the mutation rate of *Taraxacum* has been appreciably greater than that of *Antennaria*, and that of *Erophila* has probably been greater than that of *Capsella*. Yet the seed production of *Taraxacum* and *Capsella* are respectively greater than of *Antennaria* and *Erophila*.

Thus, in so far as the data permit us to judge, any correlation, if such there be, is more probably positive than negative: a relation that might merely imply a similar percentage rate in different species, so that the actual production of mutants would augment with the seed output.

That mutation rates of species can be accelerated by various external

agencies, such, for instance, as X-rays, is well known. The augmented frequency of mutations in plants raised from old seed as compared with fresh seed has been demonstrated in both *Antirrhinum* (H. Stubbe, 1935, *Biol. Zentralbl.*, 55, pp. 209–15) and *Datura* (Cartledge, J. L., and Blakeslee, A. F., 1934, *Proc. Nat. Acad. Sci.* U.S.A., 20, pp. 103–10), where it exceeds the expected increase on the assumption that the decreasing proportion of viable seeds with increasing age includes all those capable of producing mutants in the fresh seed. Thus there is at least one natural agency which may cause variation in the absolute number of mutations, and, whether dormancy be natural or induced, the number of seeds which remains ungerminated until a lapse of several years will tend to augment with the seed production.

Ageing, like X-rays, heat, and other influences found to affect the proportion of mutants, appears to operate most effectually when near the threshold of injury, a fact which may imply a compensatory benefit accompanying sensitivity to environmental changes. But be this as it may, there is no reason to regard mutation rates as significantly correlated with the evolution of different rates of reproduction.

# XVII

# VEGETATIVE MULTIPLICATION IN RELATION TO COMPETITION

The vegetative methods of propagation of flowering plants are extremely diverse, but for our present purpose we need only consider their more general features and a selection of particular examples. By contrast with reproduction from seeds the daughter " individuals " are in effect portions of the original parent and, apart from the rare occurrence of vegetative mutation usually associated with hybrid origin of the parent stock, the vegetatively produced " individuals " are hereditarily all alike. The seedlings of a pure strain, on the other hand, may exhibit some degree of heritable variation as an outcome of chromosome or gene mutations that had taken place during the formation of the gametes. It follows, therefore, that in a favourable and unchanged environment vegetative propagation is advantageous, since there will be no production of less suitable types. If, however, the environment is not stable—and such is the more normal condition—multiplication by seedlings gives a greater chance of survival should the change in the environment be in a direction less favourable to the growth of the parent stock.

The second general feature to be noted is that the modes of vegetative propagation usually result in the production of daughter " individuals " that are close to, or not far removed from, the parent individual or from one another. Thus, competition may be much more severe than amongst the seedlings, since the dispersal of the seeds is often highly efficient and the resultant seedlings widely scattered. On the other hand, it must be remembered that, except in comparatively open habitats, the daughter individual is inevitably subject to competition; and in shaded environments competition with individuals of the same species, which have precisely similar demands and attain the same stature, may be far less detrimental than the competition of species that have a greater potential stature and a leaf canopy that can effectively diminish the essential supply of light reaching their shorter neighbours. Thus, once in occupation of a shaded habitat, the larger the area a species can colonize with a continuous carpet of its vegetative organs the less the danger of seedlings of more vigorous species gaining occupancy.

Certain aspects of the physiology of reproduction are of importance in this connection. In general the light intensity necessary for satisfactory vegetative growth is appreciably lower than that requisite for the production of flowers or fruit, and this appears to apply also to temperature. As a consequence, in shaded habitats, where vegetative multiplication is most advantageous, the conditions are most favourable to this form of reproduction.

In well illuminated habitats, where the plant is making food vigorously, vegetative growth will be favoured by an abundant supply of water and nutrient salts, whilst a deficiency in water and mineral nutrients encourages flower formation.

These facts are no doubt related to the well-known influence on fruit formation of the ratio between the supply of carbohydrates produced in photosynthesis and the supply of nitrates. When the carbohydrate/nitrogen ratio is relatively low the balance is in favour of vegetative growth, whereas with a higher ratio fruit formation is favoured. The significance of the horticultural practice of root-pruning is probably that by reducing the intake of water and mineral nutrients, especially nitrates, it brings about fruiting because a higher carbohydrate/nitrogen ratio is thereby induced. But it is evident that curtailment of the root system, with like effect, might be brought about by natural causes, such as the physical conditions of the soil or the diminution in root development that is an outcome of competition.

But it is not unreasonable to suppose that the intake of trace elements, of which the importance has been demonstrated during recent years, should depend in part upon the extent of the root-system and on the absorbing surface which it presents to the soil. If this be so then any curtailment of the root system would inevitably result in a diminution of their intake. A recent study by C. S. Piper (1941, *Jour. Agr. Sci.*) has shown that a partial deficiency of manganese can inhibit healthy seed development by the plant, although there is a sufficiency of the trace element to permit of its normal vegetative growth.

Such differential response might apply to other nutrients also, and complications of this character must clearly be taken into consideration in any assessment of the extent to which the carbohydrate/nitrogen ratio affects the balance between vegetative extension and reproduction on the one hand and on the other the formation and maturation of fruits and seeds.

Since, in general, the physiological requirements for reproduction by seed demand a higher temperature than that requisite for growth it follows that vegetative propagation tends to be favoured at high altitudes and high latitudes. Thus we find that *Polygonum viviparum*, which reproduces by bulbils, has been recorded as growing on Mount Everest at an altitude of 14,500 feet, whilst the bulbiferous *Saxifraga cernua* is a common feature of the arctic regions. But two herbaceous species of *Rubus* afford an interesting comparison of behaviour. The Cloudberry (*Rubus chamaemorus*), according to Resvoll (1925), does not usually fruit well more frequently than once every seven to twelve years, and seedlings in natural conditions are rare. The flowers are unisexual, and often male flowers alone develop to maturity, since the female flowers are more susceptible to adverse climatic conditions (Resvoll, 1929). Thus, in the exposed situations that the Cloudberry normally occupies towards its southern limits, as well as in the arctic, multiplication s chiefly by means of suckers, which may attain a length of 1·7 metres (5 ft. 3 in.).

*Rubus arcticus* is also an herbaceous species which spreads rapidly by suckers, but which, though producing fertile seed in the northern part of its range, produces sterile fruits only in the southern. Such facts indicate that the preponderance of either the one or the other type of reproduction is profoundly influenced by external conditions, but the response to these is individual to the species concerned. It may be emphasized that the apomictic

species of Alchemilla, Antennaria, Hieracium, Thalictrum, etc., so characteristic of arctic and alpine regions, are in fact species in which, though the response to normal environmental conditions is reproduction by seed, yet the contained embryos are vegetative in their origin. It must indeed be recognized that the normal physiological response of plants to particular stimuli is but a means to an end and subject to modification or even reversal whenever such response fails to achieve the end upon which survival depends.

Another general feature of considerable importance is that vegetative methods of propagation are very commonly associated with the provision for the vegetatively produced offspring of a larger food supply than that associated with seed formation. This larger supply may be due to the larger size of a detached propagule, as, for example, in the bulbils of the Coral root (*Dentaria bulbifera*) or the tubers of the Potato, or it may be an outcome of prolonged attachment to the parent plant, as, for instance, in the root-suckers of the Plum or Elm. This more abundant provision implies a greater capacity to withstand initial competition, and hence we find that Elm suckers, or even those of such herbaceous plants as the Yellow Toadflax (*Linaria vulgaris*) and the Perforate St. John's Wort (*Hypericum perforatum*), can extend farther and farther into an already closed grassland community. It is largely for this reason that *Hypericum perforatum* has become such a pest in New Zealand.

The foregoing considerations show that there are certain advantages attendant upon vegetative propagation, and that these are more important in particular types of habitat. Further, that external conditions can induce either more active seed production or vegetative growth in those species which are capable of either. But it must be emphasized that there are many species that exhibit little plasticity in this respect, and which may be regarded as specialized mainly or completely to one method of reproduction, and thus perhaps better suited for a particular type of habitat and less so for others. Many species of open habitats reproduce exclusively by seed, whereas, as might be anticipated from what has already been stated, woodland species are particularly prone to vegetative propagation, and some exclusively so.

Inasmuch as both methods of reproduction entail a drain upon the parental food resources, and since the physiological conditions most favourable to the one are not identical with those most favourable for the other, it is a natural consequence that there should appear to be a certain measure of antagonism between the two methods in the sense that where both are possible abundant seed production is usually accompanied by meagre vegetative propagation, and *vice versa*. Studies of runner production by horticultural varieties of the Strawberry (G. M. Darrow, 1929) have shown that these differ markedly with respect to the number and length of the runners produced and in their tendency to branch. Entire removal of runners brought about an increase of more than double the number of fruits, and the relation between vegetative multiplication and seed production is further emphasized by the fact that ever-bearing varieties of Strawberry produce few or no runners.

The greater Periwinkle, *Vinca major*, like the Strawberry, spreads freely by means of its long runners which root at the tips, but very rarely does the

plant produce fruit. Loudon (1844, p. 1,255) states, however, that if ripe seeds are required the plants should be placed in pots with very little earth and the lateral shoots removed, which indicates that here also the balance between vegetative propagation and seed production is susceptible to modification.

But such apparent antagonism is by no means universally as marked, and some of those species which are so physiologically adjusted that they can produce good crops of fertile seed and exhibit active vegetative multiplication under the same environmental conditions are amongst the most successful in the struggle for existence in natural habitats. Examples are furnished by the Fireweed (*Epilobium angustifolium*), the Nettle (*Urtica dioica*), the Coltsfoot (*Tussilago farfara*), and the Creeping Sorrel (*Rumex acetosella*). Amongst the ferns, the Bracken (*Pteridium aquilinum*) affords a striking example, reproducing far more commonly than is often supposed by means of its wind-born spores, and, once established, spreading by its rhizomes to such an extent as to become a serious menace to agriculture.

A. De Candolle, in his " Geographie Botanique Raisonee " (Paris, 1855), enumerated on the basis of the data then available 117 species of flowering plants with a vast geographical range, being found in an area extending over at least a third of the earth's surface. Occurrence over such a wide area implies not merely a considerable range of tolerance of climatic conditions, which was the aspect that interested De Candolle, but also efficient reproduction under conditions often far removed from the optimum. A large proportion, nearly half, of these species are annual weeds of cultivated ground or disturbed soil dependent upon seeds alone, a slightly smaller proportion are aquatic or marsh plants, many of which (such as *Hippuris vulgaris*, *Menyanthes trifoliata*, *Polygonum amphibium*, *Typha* species *Sagittaria sagitifolia*, *Scirpus lacustris*, etc.) are conspicuous for their vegetative spread. Of the remaining twenty-eight perennial species of terrestrial habitats it is significant that no less than eighteen are species with conspicuously successful vegetative modes of increase.

The flora of Great Britain exhibits the same features. There are just over 260 species of flowering plants which are common in most or all the counties and vice-counties of England and Scotland, of which some eighty-three are annuals of disturbed soil and need not therefore concern us. Of the remaining, perennial, species those which possess only very slight capacity for vegetative increase, or none, comprise less than sixty species, whilst those with pronounced vegetative propagation number one hundred and twenty.

The rate of spread by vegetative means is very commonly dependent on the radial extension by means of rhizomes, stolons, etc. In one and the same species the rate of spread will be dependent partly on the vigour of the parent individual but also on the soil texture and the consequent physical resistance to be overcome during the passage of the organ through the soil. In undisturbed soils the resistance to penetration is normally least towards the surface and increases with depth. As most rhizomes and stolons grow at a level which is characteristic for the species in a particular soil type, the resistance they encounter is similar during their more or less horizontal course and

diminishes as the apex grows upwards towards the surface prior to producing a leafy aerial shoot. The stouter the rhizome or stolon the greater usually is the resistance it can overcome, so that, in general, species with slender rhizomes (*e.g. Oxalis acetosella*) are characteristic of loose superficial horizons of the soil, whilst stout rhizomes, such as those of the Bracken, are more deeply situated. The stout, slowly growing rhizome, 2 cm. or more in diameter, of the Cuckoo Pint (*Arum maculatum*) may be situated, even in heavy soils, at a depth of over a foot from the surface, where the resistance encountered during growth is very considerable. Comparative measurements of rhizome increments of the same species in heavier and lighter types of soil show that the annual increment is considerably influenced by this factor. The effect is strikingly illustrated when stolons from the base of the same aerial shoot pass either into soil or into loose leaf litter. In *Stachys sylvatica* the mean length of stolons growing in clay was 10·24 cm. (standard error 0·556), whilst the mean for plants growing in leaf-mould was 13·7 cm. (S.E.M. 0·69). This species often produces " stolons " both above and below the surface of the ground; the former, when covered by loose leaf litter, are entirely comparable with the stolons proper, except in so far as the resistance which they encounter during growth is negligible. Measurements of a number of such showed their average length to be rather more than twice that of the stolons proper.

It must be recognized that differences in soil texture, though operating in large part mechanically, may also operate physiologically. According to H. W. Laing's observations (1941) the rhizomes of *Typha latifolia* grow best in 4·6 per cent of oxygen, whilst those of *Acorus calamus* require 10 per cent. The rhizomes of *Nuphar advenum* grew well in an atmosphere devoid of oxygen. These results suggest that soil aeration may play an appreciable part in determining the annual increments of underground organs.

We can infer from such observations that soil differences will have a differentiating influence upon the competitive efficiency of species in two ways. First, by reason of stimulating or depressing the growth of one species more than another through differences in the supply of soil nutrients, air, and water; secondly, by the resistance to penetration. A marked example of this combined effect was afforded by the colonization of the waste-tip at the southern entrance to Elstree Tunnel, which I examined by courtesy of the L.M.S. Railway Co. in June, 1914. One area consisted of stiff clay and another immediately adjoining mainly of loose soil with ashes. On both areas Coltsfoot (*Tussilago farfara*) and Nettle (*Urtica dioica*) were present; but whereas on the stiff clay the former was dominant (*cf.* Plate VI) and the latter quite subordinate, on the relatively easily penetrated ash soil the conditions were reversed, the Nettles here forming an almost continuous thicket (*cf.* Plate VI) in which Coltsfoot plants were not infrequent.

According to the data given by Kerner (" The Natural History of Plants," 1904, Eng. Ed., p. 794), which presumably represent average values, the annual increments of the Nettle are between 35 and 45 cm. compared with 60 to 75 cm. for the Coltsfoot. The latter has therefore the potential advantage in this respect; but though the radial spread of this species is the greater the rhizomes of the Nettle are more richly branched, and, colonizing with rapidity in a

PLATE VI

Continuous community of Stinging Nettles (*Urtica dioica* L.) on ashes dump. The bushes are Elder (*Sambucus nigra* L.).

Coltsfoot (*Tussilago farfara* L.) colonizing clay dump.

comparatively loose soil, its greater stature effectually prevented active growth of the much shorter Coltsfoot.

Slow rate of spread is often associated with continuity of occupation, whereas rapid peripheral extension is generally associated with unshaded areas between the new shoots arising along and at the ends of the radiating stolons or rhizomes, and such unshaded areas are readily colonized by other species.

It is evident that the tendency to produce branches of the second or higher order will promote a more social habit advantageous to the exclusion of other competitors. The main rooting usually corresponds in distribution with shoot production, so that competition for water and soil nutrients is spatially similar to that for radiant energy.

The production of new shoots at the ends of a branching rhizome or from stolons clearly provides a means of separating the vegetatively produced offspring from the parent and from one another, which ameliorates the severity of competition. Where the stolon, as in *Trientalis europea*, or the rhizome, as in *Oxalis acetosella*, is very slender its main function is obviously that of an organ of migration. The absence of any appreciable migratory mechanism results in the crowding of the vegetatively produced offspring. This is a marked feature of many geophytes, as, for example, *Colchicum autumnale* and *Allium ursinum*, and may have its own peculiar advantages in continuity of occupation and preclusion of colonization by other species. Even bulbous plants may evolve migratory mechanisms, as is shown by *Scilla Adlami*, a native of Natal, in which buds are produced in the axil of the outer bulb scale. Such a bud normally develops as a rhizome, at the end of which the new bulb is formed (Chouard, 1934). There can be little doubt that, in general, such migratory capacity is advantageous, and when associated with great vegetative vigour is not merely an amelioration of intraspecific competition but a positive asset for aggression. The great success of *Spartina Townsendi* (F. W. Oliver, 1924), which is in such marked contrast to the rarity of *S. alterniflora* or the subordinate role of *S. stricta*, the two species which are its putative parents, is due to its vegetative vigour, which is almost certainly a concomitant of its hybrid origin.

Very rapid extension, with its sequel the open occupation of an area, might be thought disadvantageous as rendering the species more liable to competition; but for pioneer species in more or less open habitats the lessened competition for light between the vegetatively produced shoots and the larger volume of soil exploited for nutrition may well, by promoting more rapid growth, compensate for the risks of competition through occupation of the interstices between the radiating shoots by other species before being filled by the plant itself.

The efficacy of the vegetative mode of propagation is sufficiently witnessed by the continuous carpets or localized islands of social species which characterize most of the more closed types of community. One need only cite the large areas dominated by Dog's Mercury (*Mercurialis perennis*), Wood Anemone (*Anemone nemorosa*), Wild Garlic (*Allium ursinum*), Bracken (*Pteridium aquilinum*), as well as many others, and recall their comparative stability, to

apprehend their efficiency in preventing colonization by other herbaceous types.

It is worth noting that in our own flora there are several very successful species which reproduce exclusively, or mainly, by vegetative means, and which are characteristic of shaded habitats. Amongst such may be mentioned the Coral-Root (*Dentaria bulbifera*), the Wood Cress (*Nasturtium sylvestre*), the Lesser Celandine (*Ficaria verna var. bulbifera*), and Dog's Mercury (*M. perennis*). The first-named reproduces by means of bulbils, which replace the lower flowers in the inflorescence. The upper flowers produce pods, which, however, rarely contain fertile seeds. The bulbils, when mature, may be a centimetre in length and about three millimetres in thickness, so that though dispersed to some extent by rainwash they normally develop near the parent plant. Vegetative spread also takes place by means of the rhizome, but only slowly, as the annual increments are not usually more than 5–6 cm., and rarely exceed 12 cm. In correspondence with these facts *Dentaria bulbifera*, though quite abundant in some of the Chiltern beechwoods, is very localized in its occurrence, though many of the woodlands where it is not present would appear to be in every way suited for its growth.

*Nasturtium sylvestre* also rarely produces fertile seeds, although it flowers freely. It spreads by prostrate stems which root at the nodes, and to a limited extent by adventitious shoots upon the roots. The seeds are quite small—especially so for a shade species. This, too, is a local plant, though sometimes quite abundant over a restricted area.

*Ficaria verna* occurs in two varieties, the one producing seed and the other (*var. bulbifera*) forming little or no seed and multiplying by means of axillary buds which become detached after developing a much swollen adventitious root filled with starch. The *var. bulbifera* is very abundant, and probably more so than the variety which reproduces by seeds. *Mercurialis perennis* spreads mainly by means of its branched rhizomes, which, even in stiff clay-with-flints, will exhibit an average annual increment of 10–15 cm. per annum, whilst in less resistant types of soil the annual increments will average from 25–30 cm. per annum. As Mukerji (*loc. cit.*) showed, this species does in fact reproduce by seed, although the output is very small; but their large size precludes their ready transport, except for short distances. The abundance and high frequency of *M. perennis* can therefore be mainly attributed to its vegetative multiplication by growth and branching of the rhizomes, each of the nodes of which forms roots whilst the internodes decay after four to five years, thus conferring individuality upon the ramifications of the rhizome system.

A woodland plant that flowers profusely but produces seed rather sparsely is the Yellow Pimpernel, *Lysimachia nemorum*, but its vegetative spread by the nodal rooting of its prostrate shoots (up to 45 cm.) often renders the species locally abundant. The Lesser Periwinkle, *Vinca minor*, very rarely fruits in this country, although it too will flower freely in the woods on the more basic types of soil to which it is native; but it spreads rapidly by means of the runners, especially when the light intensity is too low to induce abundant flowering.

The rather rare Yellow Star of Bethlehem, *Gagea lutea*, also flowers well, but fruits very sparsely, in favourable seasons only, although, like *Vinca minor*, it fruits much more freely on the continent. The seeds of *Vinca minor* are relatively large (*ca.* 6 mm. $\times$2 mm.), but those of the other two species small, especially for woodland types; but the seedlings of all three appear only to become established where the light intensity is at least temporarily high. In common with other woodland herbaceous plants that fruit rarely, such as those previously referred to, the species just mentioned are often very localized, although their vegetative spread may lead to considerable colonies within the restricted areas.

Of species which have a rapid method of vegetative increase and also reproduce freely by means of seeds, the Fireweed (*Epilobium angustifolium*) is a striking example. Formerly far less common than to-day, it is now a conspicuous feature, often dominant over large areas, of heaths and woodland. The seeds themselves are quite small, and only suited to germination in more open situations; but once the seedling is established, and has formed adequate food reserves, it spreads by means of its stolons sometimes more than a metre a year. By the latter means it can penetrate into comparatively dense vegetation, and as its stems attain a height of up to two metres nourished by the parental food supply they can emerge above most other occupants. The fact that the much increased frequency of heath fires and the more extensive cutting of wood has led to a marked extension of its range and far greater abundance serves to emphasize the efficiency of the two modes of reproduction under different conditions. It is similarly true that the seedlings of the Creeping Thistle (*Cirsium arvense*) [1] only develop in comparatively open situations, whereas its vegetative extension into the densest herbage is all too familiar. The radial extension of the Creeping Thistle can, according to Rogers (1909), be as much as 20–40 ft. in a single season (*ca.* 6–12 m.). Fortunately its reproduction by seed is often slight or non-existent, owing to all the flowers on any individual plant being either functionally male or female though structurally hermaphrodite. By vegetative extension a single individual may spread over a large area, and hence, if functionally female, large quantities of thistle down might be formed but the attached fruits would be wholly infertile. According to Hayden (1934) fruit is set freely only when the plants of the two sexes are within 100 ft. (*ca.* 30 m.) of one another. According to Kolokolnikov (1931), although this species extends as far north as 68° 50′ N. flowering does not occur between 58° and 59°, whilst Malzew (1931) states that seeds require a high temperature of 25° C. to 30° C. for optimum germination.

It will be patent that extension by means of rhizomes or stolons is an effective means of invasion which depends in no small degree on the extent to which the leafy shoots formed therefrom can shade their neighbours. Thus, the potential height of the shoot and the total leaf surface it can form determine the species capable of being suppressed.

[1] According to Gill's experiments the germination of *Cirsium arvense* is only 38 per cent (Gill, 1938) whilst Kempski only obtained 11 per cent. Hayden (1934) records 10 per cent to 95 per cent.

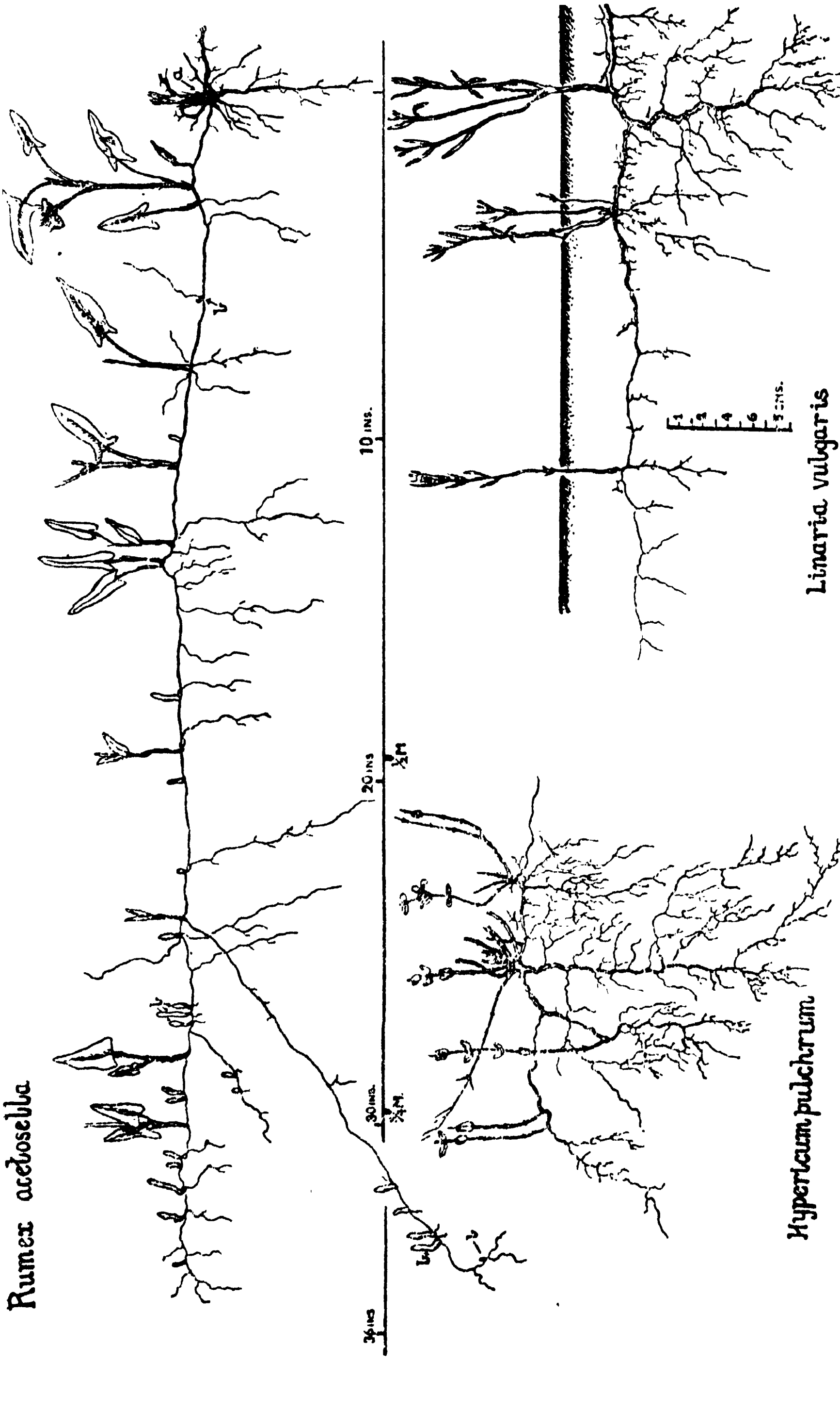
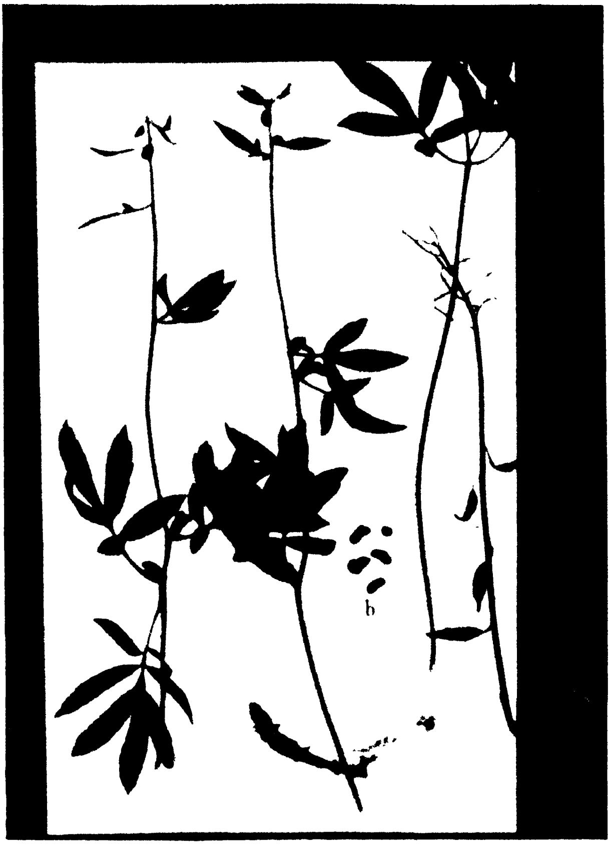
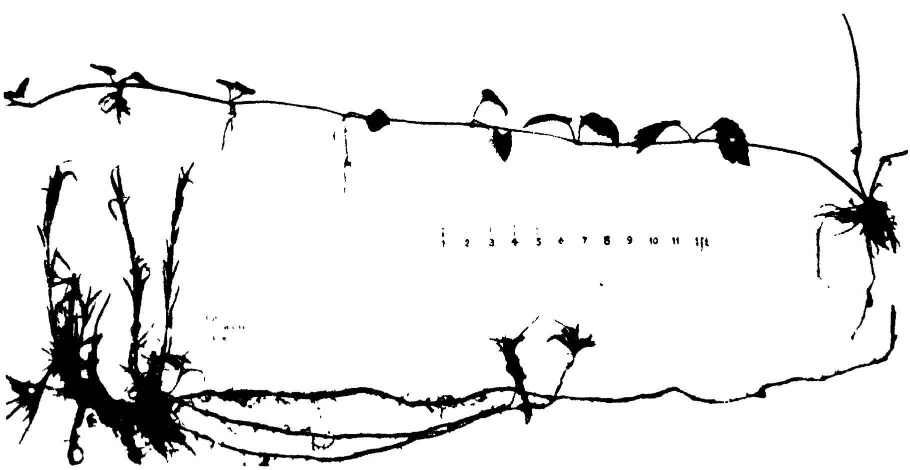



FIG. 32. Vegetative multiplication by shoots arising from roots (× ⅙).




Coral Root (*Dentaria bulbifera*) showing the bulbils which develop in the axils of the upper leaves. An inflorescence which bears abortive pods is seen on the right and at (b) a group of detached bulbils.




Above, a " runner " of the Yellow Dead-Nettle (*Galeobdolon luteum*) 37 in. in length. Below, stolons of the woodland grass, *Holcus mollis*, the longest 31 in. and two others 16 in. and 18 in. in length.

The Bishops Weed (*Aegopodium podagraria*) is a pernicious garden pest not so much because it is capable of a radial increment of more than 30 cm. per annum as because its foliage casts an effective shade. But since the major part of the foliage is radical *Aegopodium* can only suppress vegetation of comparatively low stature.

An interesting type of vegetative propagation is that due to the formation of buds upon the roots. The Creeping Sorrel is a familiar example, in which the more superficial lateral roots, sometimes extending to a distance of nearly a metre from the parent plant (see Fig. 32), bear numerous adventitious buds. Each of these when it develops forms a root system, so that a network of roots soon colonizes the ground. These laterals are often no thicker than a fine cotton thread when buds first develop upon them. The extension is thus considerable in proportion to the expenditure of material. A similar mode of reproduction is shown by *Hypericum pulchrum* and *Linaria vulgaris* (Fig. 32). The examples of these species figured were obtained from specimens colonizing closed grassland. Other species which also exhibit shoot development upon the lateral roots are *Hypericum perforatum*, *Euphorbia cyparissias*, and *Sambucus ebulus*. Amongst trees this feature is shown by the Elm (*Ulmus campestris*) and the Aspen (*Populus tremula*). The former rarely produces fertile seed in this country and the latter probably never. In view of the comparatively slender roots of these plants, trees as well as herbs, when they first penetrate the soil it is scarcely surprising that they achieve their most successful colonization on the lighter and more permeable soils.

The spectacular increase of water plants by vegetative propagation alone is due in part to the favourability of the environment for volume increase, in part to the facility with which water currents can transport comparatively bulky propagules. It must not, however, be overlooked that the environmental conditions tend towards promoting a carbohydrate/nitrogen balance favourable to vegetative growth rather than seed production.

Rhizomatous marsh plants not only spread in an environment that is physiologically favourable, unless the aeration be deficient, but also physically, as the mud offers but slight resistance to penetration. Examination of one hundred rhizome increments of *Carex paludosa* spreading into the unoccupied mud of a pond showed an average radial extension of nearly twenty-six centimetres. The variation in length of these annual increments is shown graphically in Fig. 33, from which it is seen that less than a quarter of these were under 20 cm., whilst more than one-third were 30 cm. or over. The annual increments of *Hippuris vulgaris* may attain nearly two metres in length, and increments of 70 to 80 cm. are quite frequent.

Attention may be called to the fact that, amongst the species of *Carex*, the tussock Sedges are in general those most readily raised from seed whereas the creeping Sedges which spread readily by means of their rhizomes are mostly difficult to germinate and their seedlings are not often met with under natural conditions.

The astounding spread of the Canadian Pondweed (*Elodea canadensis*), soon after its first appearance at Market Harborough in 1845, to most of the waterways of England, or the rapidity with which the Water Soldier (*Stratiotes

*aloides*) will completely occupy a pond into which it has been introduced, are the more striking, as neither normally forms seed in Britain; and this is usually likewise true for the Duckweeds (*Lemna* species), the Frog Bit (*Hydrocharis morsus-ranae*), and the Sweet Flag (*Acorus calamus*). Of these the Duckweeds flower and fruit rarely, with the exception of *Lemna polyrhiza*, which has not been recorded in flower in this country. The Sweet Flag flowers freely but does not fruit. In favourable seasons both the Water Soldier and the Canadian Pondweed may produce plenty of bloom, but the former never and the latter rarely produces fruit. The Water Soldier in this country usually produces

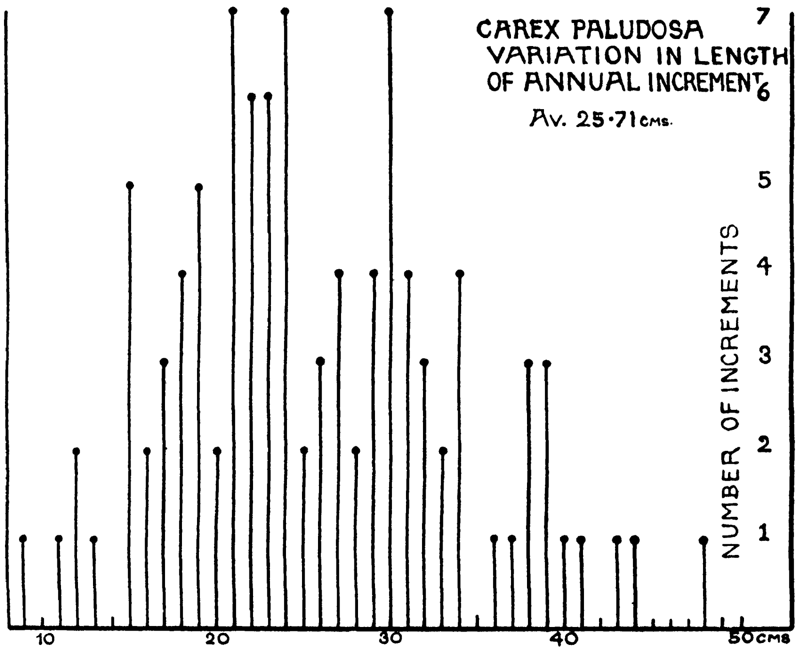



FIG. 33. Diagram showing the variation in length of the annual increments of the rhizomes of the Sedge *Carex paludosa*. Ordinates represent the number of increments and abscissae the lengths of the increments in centimetres.

female flowers only, but since hermaphrodite flowers have also been recorded (Geldart, 1906) and fruits were obtained by Clement Reid from the Cromer Forest-bed (1897) it is reasonable to suppose that the restriction to one sex is climatic rather than accidental. The plants of *Elodea* in Britain are also almost exclusively female, but this is perhaps purely fortuitous, though it should be noted that male plants have been found near Edinburgh and might have been expected to spread, were the environment favourable to individuals of that sex. The Frogbit flowers freely, but the fruits, which are capsular, containing 2–6 seeds, are uncommon and may not enclose viable seeds (Hoar, 1932). *Litorella lacustris*, when submerged, forms extensive carpets by means of runners, and only flowers when a fall in the water-level causes it to become a land plant; which recalls the somewhat parallel instance, amongst woodland plants, of the Creeping Jenny (*Lysimachia nummularia*), which in

moist, shaded habitats spreads by runners alone, whilst in dry, sunny conditions flowering is abundant.

In view of the differing optimum conditions for vegetative propagation and for reproduction by seeds not only do we find that such a species as the Yellow Dead Nettle (*Galeobdolon luteum*) spreads vegetatively (*cf.* Plate VII) in a shady woodland yet seeds freely when the undergrowth of the same wood is coppiced, but also that the balance between these two methods of increase is altered in favour of the one or the other by climatic conditions. This is well shown by a comparison of the plants of this species occupying the same area, which were examined in two successive seasons, the first being characterized by a dry, sunny summer and the second by a wet summer. The locus was in partial shade, and in the dry summer fruits were freely produced, whilst in the wet summer the number of fruits was less than half. The average number of schizachenes per plant in the dry year was about 630 and in the wet one two hundred and forty. On the other hand, the lengths of the " runners " in the wet season ranged from 37 to 154 cm. as compared with 8 to 105 cm. on the same plants in the previous year. The data for the two seasons, grouped in class intervals of 15 cm., are given in Table CI.

TABLE CI. LENGTHS OF " RUNNERS " OF *GALEOBDOLON LUTEUM* PRODUCED BY THE SAME PLANTS IN A DRY AND A WET SEASON

| Class intervals of " runner " length in centimetres | Dry season (per cent) | Wet season (per cent) |
|---|---|---|
| 5– 20 | 4·3 | — |
| 20– 35 | 8·7 | — |
| 35– 50 | 21·7 | 8·3 |
| 50– 65 | 33·3 | 13·3 |
| 65– 80 | 18·8 | 16·6 |
| 80– 95 | 11·5 | 16·6 |
| 95–110 | 1·4 | 20·0 |
| 110–125 | — | 10·0 |
| 125–140 | — | 11·6 |
| 140–155 | — | 3·3 |

The average runner lengths for the two seasons respectively were 91·5 cm. $\pm$2·5 and 59 cm.$\pm$1·5. It will be noted, too, that the mode for the wet season corresponds with the maximum class interval for the dry one. Each plant produced from 3–4 runners in the dry season and from 4–5 in the wet one, whilst associated with the longer runners the number of rooting nodes increased as well as their distance from the parent plant and from one another. *Lithospermum purpureo-coeruleum*, a southern-continental species of the woodland margin, affords another striking example, setting little seed in wet summers but spreading vigorously by means of its overground stolons, that root at the apex, which may be over 75 cm. from the parent.

It would appear that there are a few species in which the reaction to climatic conditions is the reverse of that just cited. An example is afforded by the red-flowered Onion (*Allium carinatum* L.), a species in which the inflorescence axis normally bears both flowers and bulbils intermingled. From an experience of this species in cultivation over a period of nearly twenty years it would

seem to flower freely only in wet seasons, when the inflorescences may contain ten or more flowers, and a similar number of, or rather fewer, bulbils (see Fig. 34). In a very dry season, however, few or even no flowers may be formed, and the bulbils, though smaller, are more numerous. *Allium vineale* occurs as three varieties, of which *v. capsuliferum* has an inflorescence consisting of flowers only, whilst *A. compactum* produces no flowers but a head of numerous bulbils. The latter is a pestilential weed of dry, sandy fields, especially in the Eastern Counties, whilst *v. capsuliferum* is confined to the West, and is probably a plant of damper habitats, thus suggesting a similar physiological relationship.


FIG. 34. *Allium carinatum* showing an inflorescence bearing nine flowers and fifteen bulbils. (Natural size.)

These examples will suffice to emphasize that the possession by a species of the dual mode of reproduction not only enables it to flourish in a much wider range of habitats but also ensures success in a much wider range of climatic conditions.

Of the two species of Willowherb (*E. montanum* and *E. tetragonum*), the latter, as we have already seen, has a reproductive capacity more than twice that of the former, and possesses, moreover, a more active means of vegetative propagation. *E. montanum* produces from 1–3 offsets (average 2) at the base of the flowering shoot, which in the following season give rise to erect shoots at from 0·2 cm. to 1·5 cm. (average $0{\cdot}6 \pm 0{\cdot}09$ cm.) from the previous year's flowering axis. *E. tetragonum* forms from 2–5 offsets (average 3–4) from 1–17 cm. (average $5{\cdot}2 \pm 0{\cdot}22$ cm.) from the parent axis. In both, the plumed seeds are similar, and dispersed in the same way; but, despite this, *E. montanum* is probably rather commoner than *E. tetragonum*, possibly because the latter is less tolerant than the former of dry conditions. It is of interest to note that in Hertfordshire *Epilobium angustifolium*, which far surpasses both these species in seed output and vegetative propagation, was a rare plant when the " flora " of that county was published in 1887, the other two species being then frequent. It is only during the last thirty years that increasing facilities for colonization have led to the spectacular profusion of the Rosebay Willow-herb.

Species of low growth, in which the foliage is mainly or exclusively radical,

are clearly liable to suppression by taller species, and the marked success of some of these is probably associated with their capacity for rapid occupation of open habitats. This is well illustrated by such examples as the Cinquefoil (*Potentilla reptans*), the Silverweed (*Potentilla anserina*), and the Creeping Buttercup (*Ranunculus repens*). The rapid growth of a plant of the last-named in its first year is shown semi-diagramatically in Fig. 35, from which it will be seen that more than half a square metre was occupied by thirty-five rooting nodes, of which twenty-three bore inflorescences and twelve were vegetative.

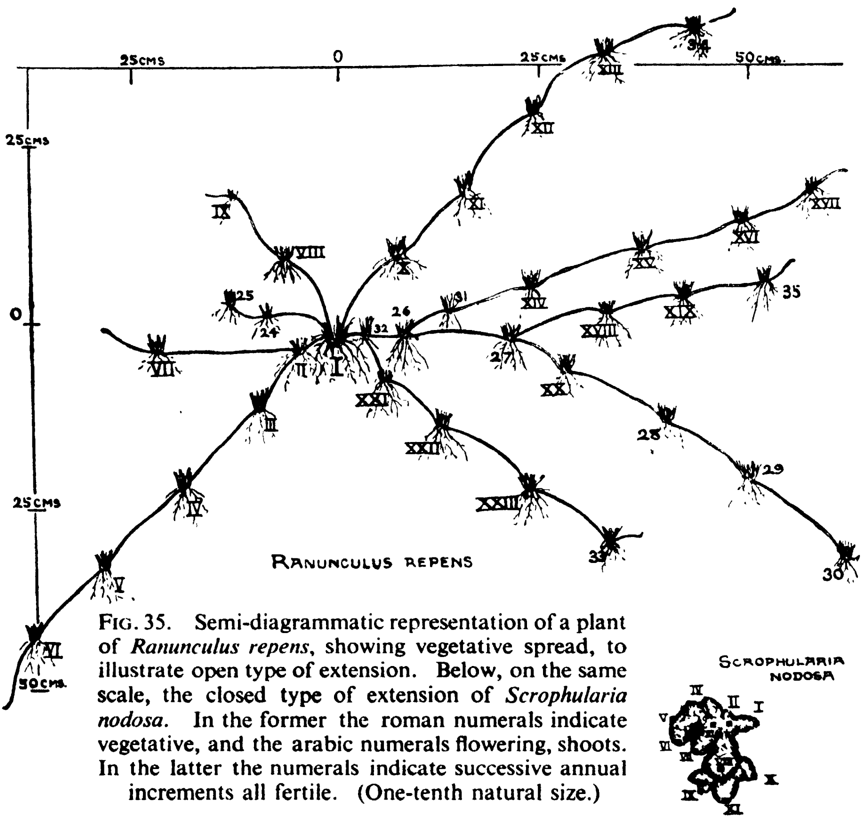



FIG. 35. Semi-diagrammatic representation of a plant of *Ranunculus repens*, showing vegetative spread, to illustrate open type of extension. Below, on the same scale, the closed type of extension of *Scrophularia nodosa*. In the former the roman numerals indicate vegetative, and the arabic numerals flowering, shoots. In the latter the numerals indicate successive annual increments all fertile. (One-tenth natural size.)

In view of the extensive vegetative increase exhibited as a normal feature by *Ranunculus repens* it will be useful to consider the data obtained for its reproduction from seed from the same soil type as the individuals of *Ranunculus bulbosus*, for which the reproduction data have already been furnished.

One hundred individuals of *Ranunculus repens* were studied for fruit production, and the range exhibited was from 0 to 38 fruit-heads per plant. The distribution was as follows: no fruit-heads (1), one (2), two (9), three (25), four (19), five (11), six (15), seven (6), eight (4), nine (1), eleven (1), twelve (2), thirteen (1), fifteen (1), twenty-three (1), twenty-four (1). The average was $5 \pm 0{\cdot}24$ ($\sigma$ 3·6; S.E.M. 0·36).

One hundred fruiting heads were examined for variation in the number of

fertile carpels. These ranged from 8 to 50, with an average of $30 \pm 0.64$ ($\sigma$ 9·6; S.E.M. 0·96). Most of the fruit-heads contained from 24 to 41 apparently fertile achenes, and the most frequent number was 35 (10 per cent).

These data give us an output of $150 \pm 10$ achenes per plant. It is interesting to compare this figure with those obtained for the closely allied *Ranunculus bulbosus* grown without, and with slight, competition, viz. 687 and 302 achenes per plant respectively. Since the *Ranunculus repens* plants grew almost exclusively under conditions of slight competition or on otherwise bare soil the comparison is valid. Under conditions of marked competition *R. repens* becomes suppressed, or, if it is able to persist, as in some wet habitats, the balance is even more in the direction of vegetative increase, and seed production is often meagre or absent. The plants examined produced from 0 to 9 runners each, but there appeared to be no obvious correlation between the number of runners and the number of fruiting-heads produced.

The annual increments of *P. anserina* may be nearly a metre in length, and as many as ten such have been observed arising from a single plant. The efficacy of this rapid occupation is seen in the large areas over which *P. anserina* remains dominant despite its comparatively low growth. In marked contrast to such types as the foregoing are those species where radial extension is slow but continuity of occupation is more or less complete. The Figwort (*Scrophularia nodosa*) affords an example in which, owing to the swollen character of the short stolons and their perennial character, almost complete exploitation within the periphery is assured (see Fig. 35).

Vegetative means of propagation are then to be regarded as of great significance especially in relation to competition, and this may be further emphasised by brief reference to two outstanding plant pests. The Blackberry (*Rubus fruticosus* agg.), which is such a menace in New Zealand as to be described as "its most deleterious weed," spreads freely by seed, but, once established, the rooting tips of its arching shoots and the capacity to produce root-shoots constitute its most formidable weapons of aggression. So, too, the Prickly Pear (*Opuntia inermis*), which was estimated to be spreading at the rate of a million acres a year in Queensland and New South Wales, achieved this mainly as an outcome of vegetative propagation.

# APPENDIX

## Germination Data

*Ajuga chamaepitys* (L.) Schreb. Mr. B. T. Lowne informs me that he has obtained 53 per cent with this species.

*Rhinanthus minor* Ehrh. The average germination appears to be about 66 per cent.

## Output Data

*Actaea spicata* L. A small plant yielded 240 berries, each of which contained from 5–11 seeds (average 8·1). The output would have been *ca.* 1,900 seeds.

*Ammophila arenaria* (L.) Link. It was estimated that a young isolated clump of the Marram Grass produced 35,650 " seeds."

*Arenaria trinerva* L. The fruits produced ranged from 51 to nearly 6,000, with an average of probably about 200 capsules. The seeds per capsule ranged from 4 to 17, with an average of 12·3 0·8. The average output is probably of the order of 2,500 seeds per plant.

*Barbarea vulgaris* R. Br. The seeds in a random sample of twenty-five pods ranged from 3 to 21, with an average of 13 ±0·56. The average seed weight of 172 seeds was 0·0006 gm. The pods were only counted on one large specimen, and numbered two thousand nine hundred and fifty-nine. This would represent an output of *ca.* 38,000 seeds.

*Bupleurum tennissimum* L. A small number of plants produced from 13 to 474 mericarps, with an average of 252 ± 60 per plant.

*Carum bulbocastanum* Koch. In a small number of specimens the range was from 212 to 792 mericarps per plant, with an average of five hundred and thirty. From the very large numbers of the monocotyledonous seedlings that may be found around a parent plant in an open situation the percentage germination is probably high.

*Cochlearia danica* L. A single large plant bore 155 capsules, with from 7 to 11 seeds in each (average 8·1 ±0·2), or about 1,250 seeds.

*Erigeron canadensis* L. The largest specimen produced 6,472 capitula, and the average is perhaps about 700 when colonizing disturbed soil. The achenes per capitulum ranged from 16 to 49, with an average of 35·5 ±2·4. This implies an average output of some 25,000 fruits.

*Geranium columbinum* L. The number of seeds per plant ranged from only a few on depauperate specimens to 760 on moderately large ones. The average was 314±55.

*Inula Helenium* L. The capitula per plant of this robust species of woodland clearings ranged in number from 9 to 60, with an average of 30±5·7. The fruits were counted in only two capitula, and numbered 533 and 600 respectively, which suggests an output of some 17,000 per plant.

*Juncus compressus* Jacq. This sub-caespitose species of Rush is a colonizer of bare mud, and individual limits are not always clearly defined. The average number of fruits per inflorescence was found to be 31±4·3. The seeds in a random sample of nine fruits were: 88, 108, 110, 113, 119, 128, 148, 152, 168, or an average of 126±5. Thus, even a single inflorescence would produce an average of 3,927±697. An output of over 60,000 seeds would probably be a conservative estimate for an adult specimen.

*Ornithogalum pyrenaicum* L. Five large specimens from a Wiltshire wood were found by Mr. Marsden-Jones to yield 16, 19, 30, 31, and 43 ripe capsules (average 27·8±2·8). The numbers of seeds in twenty capsules were: 8, 9, 11 (3), 12, 16 (2), 17 (4), 18 (2), 19, 20 (2), 21 (3), an average of 16±0·6 (average 4·0; S.E.M. 0·9). These data based on large plants indicate an output of 446±61, but the average of normal sized plants would probably not exceed four hundred.

*Senecio jacobaea* L. The seed output of the Ragwort has been studied by E. Cameron (*Jour. Ecology* (1935), pp. 265–322), and by A. L. Poole and D. Cairns in New Zealand (*N.Z. Bull.* 82, *D.S.I.R.*, 1940). The British material showed an average of 70 fruits per capitulum and about 900 capitula per plant, or some 63,000 fruits showing 80 per cent germination. The New Zealand material yielded an average of about 100,000 achenes per plant and 77 per cent germination. The average reproductive capacity is probably between 50,000 and seventy-seven thousand. Vegetative increase by adventitious buds from the roots also occurs, especially following injury to the shoot.

*Seseli Libanotis* Koch. The number of mericarps was carefully estimated for a small, a medium, and a large plant, viz. 1,222, 13,202, and 41,846. It is a short-lived perennial of semi-open habitats on chalk.

*Trifolium maritimum* Huds. (*T. squamosum* L.). A moderate-sized specimen of this rare species produced 210 seeds. J. White (1912, p. 235) records that a plant bore 241 heads, with an average of 40 flowers per head. As the pods are one-seeded, if all the flowers were fertile the output would have been 9,640 seeds.

VERONICA SPECIES

*Veronica arvensis* L. The number of seeds per fruit would appear to average $18 \pm 1{\cdot}7$, whilst Eklund's average of 54 capsules per plant gives an output of 972 seeds, which is perhaps rather below that in this country. By contrast the very rare *Veronica verna* will produce on a large plant about 60 seeds, which I have sown freshly harvested from mature capsules, and the percentage germination did not exceed 77, or a reproductive capacity of forty-six. The majority of plants yield, however, appreciably less.

*Veronica officinalis* L. The number of seeds per capsule ranged from 8 to 24, with an average of $16{\cdot}2 \pm 0{\cdot}5$. The average number of fruits per plant is about 536, so that the average output would be about eight thousand seven hundred. Germination is high (*ca.* 98 per cent).

*Epipactis palustris* (L.) Crantz. Although no complete data are available it may be worth noting that the average number of capsules developing on an inflorescence is seven to eight. The contents of one capsule yielded 2,416, apparently viable, seeds. So that the output of a single inflorescence might average about 18,000 seeds.

*Trientalis europaea* (p. 182). Matthews (*J. Bot.* p. 12, 1942) reports average germination as 78% with more rapid and slightly higher germination in light. Compared with the populations examined by me his material produced half the number of fruits but twice as many seeds per fruit, an average output of 8 instead of 7 seeds per plant.

# SUMMARY

The present work is a preliminary contribution to the quantitative study of one most important aspect of the biology of the higher plants, in which we have attempted to find an answer to the questions raised in the introductory section. It is obvious from a perusal of these pages that the average and potential progenies of a species are as much a specific characteristic as its average and potential heights, though, like the latter, subject to a considerable range of normal variation.

Data are here furnished, for the first time, respecting the seed production of over two hundred and forty British species, the publication of which will, it is hoped, serve as a basis for augmentation by other investigators. Although for some few of these species the number of specimens examined is insufficient to provide more than a tentative estimate of their productivity, the general conclusions represent the outcome of the examination of some hundreds of thousands of individual plants and of considerably more than three-quarters of a million of their fruits.

In addition data, resulting from some hundreds of germination experiments, concerning the normal viability of the seeds of many of the species investigated are also provided, so that it is possible to estimate what is here termed the "average reproductive capacity" in terms of the potential progeny.

It is obvious that such a mass of data could only be accumulated over a period of years and with the help of others, but until such information is available for all the more important species of flowering plants which constitute the plant communities of a region it will be impossible to assess adequately the factors responsible for their frequency or abundance. In the meantime these pages furnish a substantial contribution to our knowledge of this aspect of the British flora.

It has been here shown that whilst the seed output of a number of individuals of a species commonly exhibits a variation that approximates to a normal variation curve there is quite frequently a marked difference between the modal value for seed output and the mean value, so that estimates based upon the examination of so-called "average specimens," however attractive as economizing time and labour, may be misleading in the extreme. This is particularly marked with respect to populations of monocarpic species, which frequently exhibit a high proportion of small individuals, so that the mean productivity of the species is very different from that of the most frequent individual in respect to size and output. Moreover, in some of these monocarpic species the variation "curve" for seed output has a mode near the lower limit, or the "curve" may even be hollow in form.

Evidence is afforded from the study of the seed and fruit weights of nearly three hundred species from different types of habitat conditions that the seed or fruit weight tends to augment with the degree of shade to which the seedling is normally subjected. In general, it would appear that the more advanced the phase of succession with which the species is naturally associated

the larger the amount of reserve food material provided in the seed. A study of the range of variation of the weights of the propagules of the different species in the several types of habitat conditions studied shows the mode to correspond to a higher value the more shaded the conditions with which the developing seedling has to contend. Such generalizations appear to be confirmed when we compare the weights of the seeds, or fruits, of pairs of species belonging to the same genus but occupying habitats differing with respect to their density and degree of shading at ground level. Consideration of the seed weights of a number of species belonging to the genus *Trifolium* shows the same feature. The most notable exceptions are furnished by species which, though associated with late phases of succession, are in fact dependent upon " light gaps," or other forms of reversion to earlier phases of the succession, for their establishment. In brief, *the capacity to colonize in the face of competition appears to be associated with the amount of food reserve which the seed contains.* This rule does not hold for parasites or saprophytes, which, by reason of their special modes of nutrition, are exempt from the inhibition of inadequate food supplies which may be imposed upon seedlings which are dependent upon light for the manufacture of food by the mere proximity of other plants. It is suggested that the mycorrhizal habit confers in varying degrees a similar immunity. The minute food reserve contained in the seeds of most parasites and saprophytes and many species with a pronounced mycorrhizal association is held to have been rendered possible without detriment to the survival value of the species by reason of their special modes of nutrition.

In view of the increased weight of the seeds of some polyploids, attention is called to their possible ecological importance in advanced communities.

The variability of seed weight within the species is discussed, and evidence is furnished to show that, for those species which possess dimorphic or polymorphic seeds or fruits, the heavier propagules do in general produce seedlings that are better able to withstand adverse conditions. In those species where the variation in seed size is continuous, the experiments by divers investigators would seem to show that the larger seeds confer an initial benefit under conditions of competition.

Experiments with two species of *Silene* and *Solanum nigrum* are described, which show that seeds derived from individuals of very diverse degrees of vigour show no significant difference in the viability of the seeds produced, and that in general the effect of adverse conditions, such as competition, unless of an extreme character, is to cause a diminution in the number of seeds per plant rather than to affect the quality of the seeds themselves.

The very great importance of competition as affecting the magnitude of the seed output is demonstrated. Hence the necessity for ascertaining the seed production of species from individuals growing under the natural conditions of their normal environment. This seed output for a particular habitat, as distinct from the far larger potential output in the absence of competition, may be an important factor in determining the occurrence of a species in natural conditions as well as its frequency or abundance.

It is shown, for various species, that over a considerable range of plant size

there is no significant correlation between the number of fruits per plant and the number of seeds per fruit.

Determinations of the seed production of species belonging to a diversity of genera show that the more ecologically restricted types, in which mortality might be expected to be highest, do not, in comparison with commoner related species, exhibit a larger output. Indeed, it may be said that the truth of the matter is almost the reverse, since those species which demand particularly restricted environmental conditions have been shown to possess the more meagre reproductive equipment whereas those species which have numerous niches or large areas they can occupy, however infrequently, and which can thus most readily profit by a large output, have in fact the capacity for a high potential progeny.

Our study of the four British species of Papaver shows that their frequencies roughly correspond to their respective reproductive capacities and their dispersal efficiencies, under comparable experimental conditions. It would, indeed, appear to be true generally that, for ecologically comparable species, the magnitude of the reproductive capacity is associated with the frequency and abundance of which it is probably one of the determining factors. On the other hand the magnitude of the reproductive capacity appears to bear little if any relation to the risks of mortality, though a certain minimum is obviously necessary to meet those risks, but it would appear probable that, for most species at least, the seed output is considerably in excess of that minimum. The seed output is to be regarded, not so much as an insurance against extinction, as an insurance against rarity, and the effective premium which the organism can afford to pay doubtless bears a definite relation to the available niches in the natural habitats that the plant can occupy.

Comparison of annual and perennial species shows that the latter usually have the higher seed output, although the risks of failure in replacement are lower for the perennial than for the annual.

Most parasites and saprophytes, as well as some semi-parasites, we have seen to possess minute seeds, and this small size, as already suggested, may have been rendered possible, without detriment to survival, owing to the methods of nutrition. The small demand which each makes upon the parent permits of a large seed output, the magnitude of which has been determined for various parasites and saprophytes. It would seem very doubtful whether the rather large output is necessitated by mortality risks, as has hitherto been tacitly assumed, but rather that it is advantageous as enabling the species to exploit the special conditions such plants require which often obtain only intermittently.

In comparison with non-parasitic species having seeds of small size the output of the parasite may actually be smaller, and if account were taken of the relative risks of mortality it is probable that the seed output of parasites could not be regarded as especially high.

A study of the British species of St. John's Worts (*Hypericum* species) indicates the positive asset of a high reproductive capacity and also the great importance of vegetative propagation, especially in relation to competition. It is also shown that the British members of the Gentianaceae exhibit a striking parallel between the average seed output and the frequency of the respective species.

Attention is called to the possible biological importance of periodic fruiting (exhibited by polycarpic types that have pronounced "mast" years, and monocarpic biennials and perennials) as a means of evading the heavy attacks of parasites and predators which might render a continuously high output, with a consequential high population level, nugatory.

Consideration of species associated with the different types of habitat conditions brings to light a marked association between the conditions for colonization and the magnitude of the seed output. The largest seed productions are characteristic of species associated with habitats that are only intermittently available for colonization, such as woodland clearings and the intermittently exposed mud of shallow lakes and ponds. Such "opportunists" in the plant world constitute a biological category not hitherto distinguished but which it is of considerable ecological importance to recognize. The average output for thirty-two species of such intermittently available habitats was about 227,000 seeds per plant. The lowest seed outputs characterize the herbaceous shade species of woodlands, in which the increased pressure of competition and shading to which the germinating seedlings are subject is met by increased seed weight and/or vegetative means of propagation.

Between the two extremes just cited the species of open habitats, continuous either in space or time, have a moderately high output, whilst the species of partially closed, unshaded, habitats and of closed but more or less unshaded habitats are characterized by progressively lower outputs.

The conclusion appears to be warranted that for most species at least the seed output is considerably in excess of that requisite for mere replacement of losses by death and sufficiently so to bear no obvious relation to the normal seedling mortality. The size of the seed output, or more precisely the reproductive capacity, is regarded as a positive asset in the competitive equipment of the species which tends to ensure occupancy of the available ecological niches and so to increase the species' frequency and abundance.

The efficacy of various types of vegetative increase are discussed and their importance in relation to competitive pressure emphasized. Vegetative propagation often provides the equivalent of a large food supply in a seed, but over a much longer period, thus permitting tolerance of greater and more prolonged competition by the vegetatively produced offspring. Examples are furnished to show that some of the most successful species are those which exhibit a large seed output and possess also a means of vegetative propagation, whilst species in which vegetative propagation is the only or dominant method of reproduction are mostly associated with the more densely populated habitats and the later phases of the plant succession.

The features of seed weight, seed output, and viability, as well as the methods of vegetative increase which we have here considered, lose nothing in the importance of their biological significance in the light of their quantitative study. But that significance is seen to be the antithesis of that attributed by Herbert Spencer and others. A high reproductive capacity, on the views hitherto orthodox, might be rightly held to be in the nature of a mark of failure, whereas the evidence furnished in the foregoing pages has shown that a high potential rate of increase is, indeed, rather a criterion of success.

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# INDEX

(Note that the majority of the species are indexed under their Latin names only. Where there is an English name this is given in parentheses after the Latin binomial.)

w. indicates average weight of seed; r. indicates reproduction data.